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Direct and Indirect Estimation of Gillnet Selection Curves of Atlantic Herring (*Clupea harengus harengus*)

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Winters, G. H., and J. P. Wheeler. 1990. Direct and indirect estimation of gillnet selection curves of Atlantic herring (*Clupea harengus harengus*). Can. J. Fish. Aquat. Sci. 47: 460–470.

Length-specific selection curves for Atlantic herring (*Clupea harengus*) were calculated for a series of gillnets ranging in mesh size from 50.8 to 76.2 mm (stretched measure) using Holt's (1963) model (ICNAF Spec. Publ. 5: 106–115). These curves were than compared with direct estimates of length-specific selectivity obtained from a comparison of gillnet catch length frequencies with population length composition data as determined from acoustic surveys. Selection curves calculated indirectly using the Holt model were unimodal and congruent. The empirical selection curves however were multimodal and fishing power varied with mesh size. These differences in selectivities were due to the fact that herring were caught not only by wedging at the maximum girth but also at other body positions such as the gills and snout. Each of these modes of capture have different length-specific selectivity characteristics and, since the relative contributions of the different modes of capture varied both between nets and annually, the selection curve of herring for a particular mesh size is not unique. It can however be reasonably approximated when girth is used as the selection criterion. Direct empirical selectivities are therefore recommended when interpreting population parameters from herring gillnet catch data.

À l'aide du modèle de Holt (1983) (ICNAF Spec. Publ. 5 : 106–115), les auteurs ont obtenu les courbes de sélectivité d'une série de filets maillants pour la pêche du hareng de l'Atlantique (*Clupea harengus*), dont la grandeur de maille variait de 50,8 mm à 76,2 mm (maille étirée). Ils ont ensuite comparé ces courbes à des estimations directes de la sélectivité obtenues par comparaison des fréquences de longueurs des prises au filet maillant et des données sur la répartition au sein de la population des longueurs obtenues par levés acoustiques. Les courbes de sélectivité calculées indirectement à l'aide du modèle de Holt étaient unimodales et congrues, mais les courbes de sélectivité empiriques étaient multimodales et la capacité de pêche variait selon la grandeur de maille. Ces différences de sélectivité s'expliquent par le fait que les harengs étaient capturés non seulement parce qu'ils étaient retenus au niveau du point de circonférence maximale du corps mais aussi par emmêlement des ouïes ou du museau dans les mailles. Chacun de ces modes de capture présente des caractéristiques particulières de sélectivité et, étant donné que la contribution relative des différents modes de capture varie selon le filet et l'année de capture, la courbe de sélectivité du hareng pour une grandeur particulière de maille n'est pas unique. On peut toutefois en obtenir une approximation raisonnable en utilisant la circonférence du corps comme critère de sélectivité. Il est donc recommandé d'utiliser des courbes de sélectivité empiriques directes pour l'interprétation de paramètres de populations de hareng calculés à partir de données sur les prises au filet maillant.

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The decline in fish meal prices and the conjunctive improvement in markets for food herring in the 1970s resulted in the increased use of gillnets in herring fisheries in the Northwest Atlantic. The expansion of gillnet fishing effort merely reflected the economy of scale and high quality product traditionally associated with commercial gillnetting (Hamley 1975). Gillnets, however, are very selective in their exploitation pattern and this has created difficulties in the interpretation of gillnet catch statistics in herring stock assessment studies (O'Boyle and Cleary 1981; Ahrens 1985). Extensive analyses of gillnet selectivities are available in the published literature for a wide variety of species (e.g. see review by Hamley (1975)). For the most part these studies have relied heavily on the classical models of Baranov (1948) and Holt (1963). Such models estimate gillnet selectivity in an indirect manner and require certain critical assumptions to be met. These include uniform catchability coefficients for nets of different mesh sizes and congruency in the shape of the selection curves. In practice, these assumptions are often violated (Pope et al. 1975) due to a variety of factors such as behavioral effects (Hamley 1975; Rudstam et al. 1984) or features of the net other than its mesh size (Riedel 1963; Stewart 1987).

In the Northwest Atlantic, Olsen (1959) has provided estimates of gillnet selection curves for Atlantic herring based on a generalization of the Holt (1963) model. In this paper we apply the Holt (1963) model, to length frequencies of herring caught in gillnets ranging in mesh size from 50.8 to 76.2 mm stretched measure. The resulting selection curves are then compared with direct estimates of selectivity obtained from a comparison of gillnet catch length frequencies with population length composition data as determined from acoustic surveys. Differences in selectivity between the direct and indirect techniques are evaluated in terms of the manner in which herring are caught and retained in gillnet fisheries.

Materials and Methods

The data used in this study were obtained from research gillnet catches of predominantly spring-spawning herring from

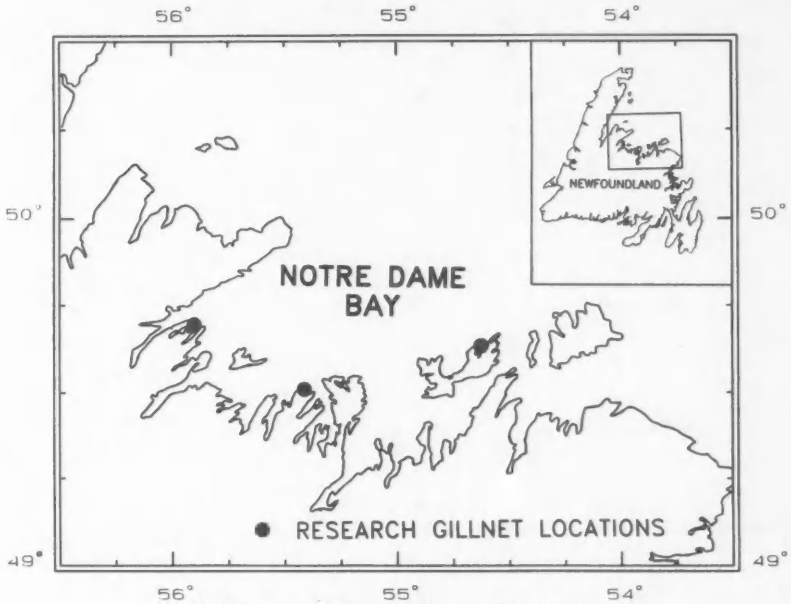

FIG. 1. Map research gillnet locations mentioned in the text.

three locations in Notre Dame Bay, Newfoundland (Fig. 1), in October of 1986 and 1987. The gillnets used were all made of multifilament nylon (210/9, green, knotted) and measured 34.3 m by 200 meshes deep with the exception of the 50.8-mm net which was 150 meshes deep. The hanging ratio (headrope length/stretched netting length) for all nets was 0.67, the same as that of commercial herring gillnets. Headrope floatation was achieved using torpedo floats and the footrope was made of light head line. Five nets of different mesh sizes were employed at each location, nominally 50.8, 57.2, 63.5, 69.9, and 76.2 mm. These were fished in gangs of two (50.8 and 57.2 mm) and three nets (63.5, 69.9, and 76.2 mm) with a gap of 1 m between adjacent nets. Tidal and wind conditions precluded fishing the five nets as a single fleet.

At each location (Fig. 1) the two gangs of nets were fished consistently as set nets, in close proximity with one end anchored to shore. The nets were fished from the surface and were hauled each day for a period of 4 wk. Total catches (in numbers) were recorded for each mesh size and random samples were selected for length, sex, and maturity data. Bycatches of species other than herring were generally less than 5% of the total catch. Catches in 1987 were separated according to the following modes of capture: (i) wedged, i.e. meshed between the operculum and the point of maximum girth; (ii) gilled, i.e. meshed at the gills; and (iii) other, i.e. tangled by the lips, snout, or otherwise trammeled. Girth measurements, obtained at the mesh mark (for wedged fish only) using a tape measure were used to estimate compressibility, i.e. the ratio of girth at the mesh mark to net perimeter. Girth measurements were also obtained at the anterior of the dorsal fin (i.e. the maximum girth) and at the rear of the operculum (i.e. the opercular girth). Sampling details of the various gillnet catches are given in Table 1. Net saturation was not considered to be a problem as maximum daily catches rarely exceeded a total of 400 fish for all nets.

Estimates of biomass and population numbers for the Notre Dame bay herring stock in October 1986 and October 1987 are available from acoustic surveys (Wheeler and Chaulk 1987; Wheeler et al. 1988). In these surveys, Notre Dame Bay was subdivided into a series of survey blocks for which population numbers were derived from line transect acoustic surveys. For each block, herring length frequency data were obtained from sets by an attendant purse seine vessel. These sets were essentially randomly chosen since sets were made along the acoustic transects whenever and wherever school size and water depth were suitable for purse seine operation. These length frequency data were used to provide a population length composition for each block. Survey block statistics were then aggregated to provide a total population length frequency for Notre Dame Bay in October 1986 and October 1987. Implicit in this procedure is the assumption that the research purse-seine samples adequately represent the length frequencies of the herring schools encountered in the acoustic survey for each block.

Indirect estimation of gillnet selection curves for each mesh size was obtained using the classical Holt (1963) model. This model requires no knowledge of the population composition but instead makes the assumption that the selectivity curves of nets of different mesh size have the same shape and amplitude. If

C_{ij} = catch of fish of length j in mesh i,
l_j = length of fish of size class j,
m_i = size of mesh in net i, and
S_{ij} = selectivity of mesh i to size class j,
$\bar{l}_i$ = mean selection length for mesh i,

then the steps in the Holt model are as follows:

1. Assume that $\bar{l}_i = \kappa m_i$ where κ is a constant.
2. For pairs of nets of adjacent mesh sizes calculate the ratio $R_{i+1,i,j}$ where

(1) $R_{i+1,i,j} = C_{i+1,j}/C_{ij}$.

3. Take the logarithm of $R_{i+1,i,j} = Y_j$ and estimate by linear regression the function $Y_j = a + bl_j$.

TABLE 1. Catch at length statistics of research gillnet operations in Notre Dame Bay for October 1986 and October 1987.

Year	Mesh size (mm)	Catch at length (cm)															Total
		26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
1987	50.8	3	3	1	1	5	66	211	117	43	21	6	—	1			478
	57.2	1	1	1	1	3	66	222	143	37	26	7	6	3			517
	63.5					2	27	87	70	37	31	22	37	16	4		333
	69.9						9	32	40	19	23	19	16	15	4	1	178
	76.2								4	7	7	5	8	7	—	1	39
	Total	4	4	2	2	10	168	552	374	143	108	59	67	42	8	2	1545
	Percent	0.3	0.3	0.1	0.1	0.6	10.9	35.8	24.2	9.3	7.0	3.8	4.3	2.7	0.5	0.1	100.0
1986	50.8			1	8	32	32	12	4	11	4	2	2				108
	57.2			1	7	38	47	13	10	14	11	1	3	2			147
	63.5				8	72	94	44	40	39	28	19	17	16	2		379
	69.9				1	21	45	32	40	78	41	28	34	19	5		344
	76.2					2	5	5	14	45	27	24	38	36	4	4	204
	Total			2	24	165	223	106	108	187	111	74	94	73	11	4	1182
	Percent			0.2	2.0	14.0	18.8	9.0	9.1	15.8	9.4	6.3	8.0	6.2	0.9	0.3	100.0

4. For each pair of mesh sizes calculate the ratio $2a/b$ and plot against the sum of the corresponding mesh sizes.
5. Using linear regression analyses, fit the best straight line passing through the origin. The slope of this line is then equal to κ.
6. Solve for $\bar{l}_i$ using the relationship $\bar{l}_i = \kappa m_i$.
7. Calculate the variance, σ_i^2 for each mesh size from

$$(2)\quad \sigma_i^2 = \frac{\bar{l}_{i+1} - \bar{l}_i}{b}$$

8. The mean variance σ^2 can then be calculated and the selectivity curves for each net are obtained by substituting σ^2, l_j and $\bar{l}_i$ in the equation

$$(3)\quad S_{ij} = e^{-\frac{1}{2\sigma^2(l_j - \bar{l}_i)^2}}$$

9. Normalized selectivities are then calculated as follows:

$$(4)\quad S_{ij} = e^{-\frac{1}{2\sigma^2(l_j - \bar{l}_i)^2}} S_{ij}\ \max$$

It was evident from purse seine sets on discrete schools of herring in Notre Dame Bay in 1986 and 1987 that, with the exception of 0-group and 1-group herring, these schools contained a heterogenous assemblage of all fish sizes. As 0-group and 1-group herring are not recruited to the gillnet mesh sizes used, size-specific encounter probability was not considered in our analyses.

The direct empirical method of estimating selectivity requires that selectivity be defined as the probability of capture by a single unit of effort, i.e. for any length j and mesh size i

$$(5)\quad S_{ij} = C_{ij}/E_i \cdot N_j,$$

where E_i = fishing effort exerted by mesh i; and N_j = population numbers of length j as estimated from acoustic surveys.

Since all mesh sizes for each experiment were fished at the same time, E_i refers to the standardized area (square metres) of each net.

Results

Catch and Population Length Frequencies

The composite length frequency of the combined mesh size catches (Fig. 2) shows that the technique of gang fishing is able to duplicate the major modes in the population length frequency for herring 27 cm and larger. The relative amplitude of the various modes are, however, somewhat distorted in the gillnet length frequencies and suggests that the larger gillnets are more efficient than the smaller nets. The length frequencies of individual mesh sizes (Table 1) are generally multimodal. In addition there is a substantial increase in the relative contribution of the smaller mesh nets to the total catches in 1987 compared with 1986. This is consistent, to a certain degree, with the decline in the relative abundance of the larger (>32

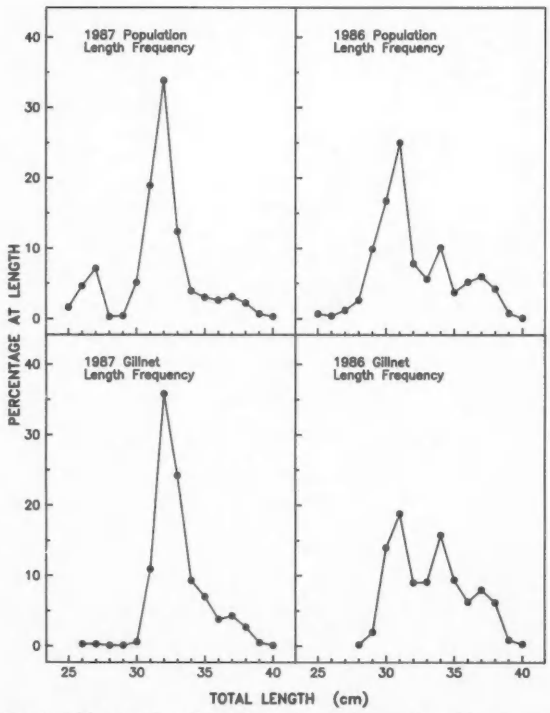

FIG. 2. Gillnet catch and population length frequencies of herring in Notre Dame Bay, 1986 and 1987.

TABLE 2. Summary statistics of the application of the Holt (1963) exponential selection model to gillnet length frequencies from Notre Dame Bay in October 1986, 1987. Sample sizes (Table 1) less than 10 for adjacent meshes were omitted from these analyses.

	Mean selection length (cm for mesh size)					Holt selection coefficients	
Year	50.8	57.2	63.5	69.9	76.2	$\bar{K}$	σ^2
1986	25.5	28.7	31.8	35.0	38.2	5.01	18.99
1987	29.1	32.7	36.3	40.0	43.6	5.72	18.43

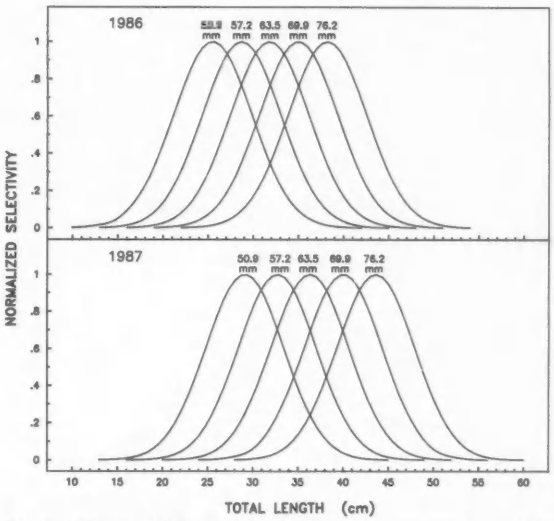

FIG. 3. 1986 and 1987 gillnet mesh selection curves as estimated by the Holt model.

cm) herring in the 1987 population length frequency (Wheeler et al. 1988).

Selectivity Estimated by the Holt Model

Summary statistics resulting from the application of the Holt model to the mesh-specific length frequencies (Table 1) for 1986 and 1987 are given in Table 2. Mean selection lengths by mesh size were substantially larger in 1987 compared with 1986. The selection curves (Fig. 3) are, of course, congruent and of equal amplitude.

Direct Estimation of Gillnet Selectivity

We shall first examine the 1987 gillnet data because ancillary data on mode of capture, girth measurements, and compressibility estimates are available. These data will allow us to evaluate more precisely patterns evident in the empirical selectivity curves.

Girth parameters

Maximum body girth and opercular girth of herring were linearly related to total length (Fig. 4). The divergence between the two lines with increasing length implies that the angle of taper may be greater in the larger fish. This would affect the overall selectivity comparisons between nets since the relative efficiency of the various modes of capture would change with fish length.

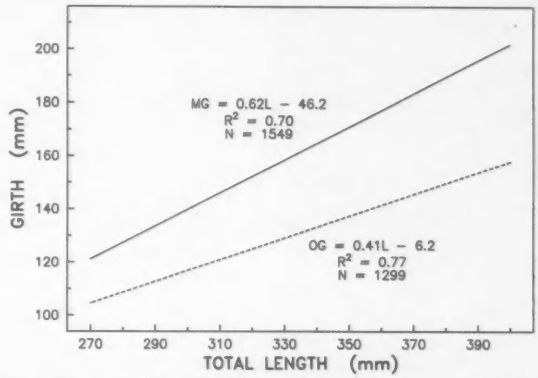

FIG. 4. Regression lines of maximum girth (MG) and opercular girth (OG) on herring length.

The relationship between maximum girth and body length by mode of capture was described by the following algorithms:

Wedged $MG = 0.61L - 44.18\ r^2 = 0.66\ n = 725$
Gilled $MG = 0.64L - 51.77\ r^2 = 0.74\ n = 613$
Other $MG = 0.55L - 22.48\ r^2 = 0.70\ n = 211$

There was a significant difference in slopes of the maximum girth–body length relationship by the various modes of capture ($P = 0.03$). However, given the large sample sizes and the marginal level of statistical significance it is doubtful whether this statistical difference can be interpreted with biological confidence. The relationship between maximum girth and body length by mesh size was described by the following algorithms:

50.8 mm $MG = 0.57L - 29.32\ r^2 = 0.56\ n = 480$
57.2 mm $MG = 0.60L - 40.88\ r^2 = 0.57\ n = 518$
63.5 mm $MG = 0.60L - 36.01\ r^2 = 0.72\ n = 334$
69.9 mm $MG = 0.53L - 14.26\ r^2 = 0.68\ n = 178$
76.2 mm $MG = 0.48L + 7.99\ r = 0.57\ n = 39$

There was no significant difference among mesh sizes in slopes of the maximum girth–body length relationship by mesh size ($P = 0.10$). However, there was a significant difference ($P < 0.001$) in this relationship between spawning groups for mature fish i.e. maturity stage IV (essentially maturing spring-spawners) and maturity stage VIII (recovering-spent fall-spawners) described by the followng algorithms:

Stage 4 $MG = 0.62\ L - 45.3\ r^2 = 0.72\ n = 757$
Stage 8 $MG = 0.46\ L - 0.5\ r^2 = 0.61\ n = 79$

Thus variations in spawning group composition (and, by implication, body condition) will act to confound selectivity curves when length is used as the measure of body size.

Compressibility, defined as the ratio of girth at the mesh mark to net perimeter, declined with increase in mesh size (Fig. 5). In addition, compressibility varied according to the location of the mesh mark (Fig. 6), being greatest at the point of maximum girth and smallest at the snout. With respect to Fig. 5, because mesh size and mean length of fish caught are highly correlated, it was not possible to separate the confounding effects of these two variables on compressibility. However, the fact that body taper increases with fish length (Fig. 4), suggests that the decline in compressibility with mesh size is a length-dependent effect.

In summary, there are at least three factors which will tend to complicate a simple interpretation of gillnet selectivity based

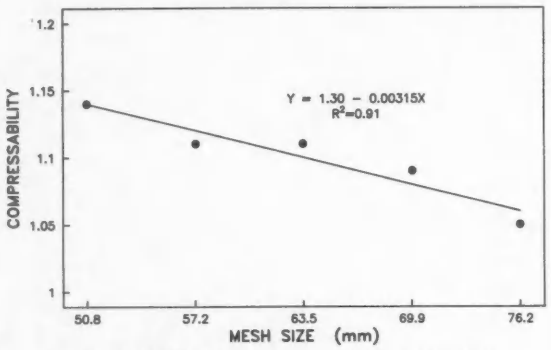

FIG. 5. Relationship between compressibility and mesh size.

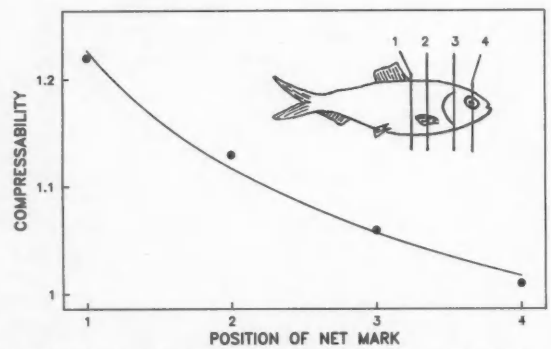

FIG. 6. Relationship between compressibility and location of the net mark.

on measurements of fish length, i.e. a change in body taper with length, spawning group composition (and therefore condition factor), and variations in compressibility related to fish length and position of capture. Similar observations were made by McCombie and Berst (1969) for a variety of freshwater fish species.

1987 mesh selectivity experiment

Empirical selectivity curves (normalized to the overall mean) estimated by expression (5) for the various mesh sizes are shown in Fig. 7 and Table 3. These curves do not conform to the principle of geometrical similarity espoused by Baranov (1948) but rather are bimodal or multimodal in a pattern of progressive escalation of amplitudes from the smallest modal size to the largest. Fishing power, as measured by the adjusted exploitation rate, was highest in the 50.8-mm mesh and lowest in the 76.2-mm mesh. In addition, given nets of a specific hang ratio, the selection range becomes progressively smaller with increase in mesh size (Fig. 8). This is due to the ability of the smaller nets to catch much larger fish than would be expected from the direct proportionality between mesh perimeter and maximum fish girth. Plots of girth-perimeter ratios by mesh size (Fig. 9) show that whereas this ratio is relatively constant for the smallest fish caught ("min" line), the ratio declines with mesh size for the larger fish caught ("max" line). This reduction in the girth–perimeter ratio is too large to be accounted for by the estimated changes in compressibility and suggests that there are modes of capture other than the classical wedging mode upon which

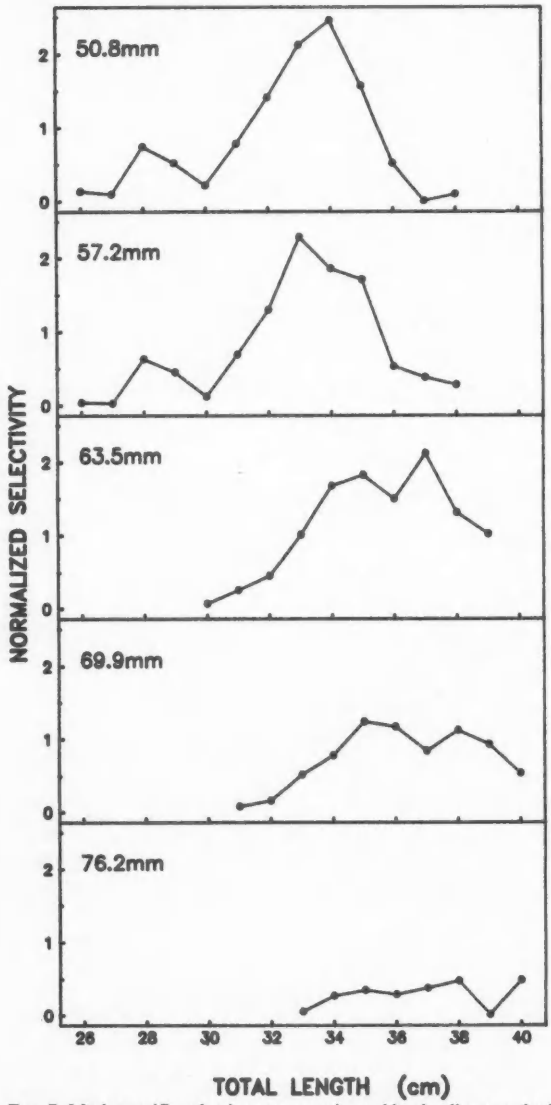

FIG. 7. Mesh-specific selection curves estimated by the direct method for 1987 gillnet samples.

the selection models of Baranov (1948) and Holt (1963) are based.

Length frequencies of herring caught by the three modes of capture are shown in Fig. 10. In general, wedging was the dominant mode of capture, although gilling was also important, particularly in the smallest mesh size. Fish caught or tangled by the snout (i.e. classed as 'others') were of importance only in the smallest mesh sizes. This is consistent with the observations of Wilson and Andrew (1987) who showed that a tight hanging ratio reduces the chance of capture by tangling. As expected, wedging tends to catch the smallest herring for any particular mesh size, followed by gilling and 'others.' This pattern is more clearly demonstrated when the combined length frequencies of the various mesh sizes are converted to a com-

TABLE 3. Length-specific exploitation rates (i.e. selectivity rate) of herring estimated directly from the 1987 gillnet data. The adjusted exploitation rate takes into account differences in net area.

Length (cm)	Population l/f ($\times 10^{-5}$)	Exploitation rate ($=\mu \times 10^{-5}$) by mesh size (mm)					Normalized selectivity ($\mu/\bar{\mu}$)				
		50.8	57.2	63.5	69.9	76.2	50.8	57.2	63.5	69.9	76.2
26	15.10	0.20	0.04				0.14	0.04			
27	23.53	0.13	0.03				0.10	0.03			
28	1.04	0.99	0.64				0.74	0.63			
29	1.45	0.70	0.46				0.52	0.45			
30	17.03	0.29	0.12	0.07			0.22	0.12	0.07		
31	62.75	1.05	0.70	0.26	0.08		0.78	0.69	0.26	0.08	
32	111.85	1.89	1.32	0.47	0.16		1.41	1.30	0.46	0.16	
33	41.03	2.85	2.32	1.02	0.53	0.05	2.13	2.29	1.01	0.52	0.05
34	13.07	3.29	1.89	1.70	0.79	0.27	2.46	1.86	1.68	0.78	0.27
35	10.01	2.10	1.73	1.85	1.26	0.35	1.57	1.71	1.83	1.24	0.35
36	8.69	0.69	0.54	1.52	1.19	0.29	0.52	0.53	1.50	1.17	0.29
37	10.30	—	0.39	2.15	0.85	0.39	—	0.38	2.12	0.84	0.38
38	7.21	0.14	0.28	1.33	1.14	0.40	0.10	0.28	1.31	1.12	0.48
39	2.32			1.03	0.94	—			1.02	0.93	—
40	1.00				0.55	0.50				0.54	0.49
No. caught		478	517	333	178	39					
Adjusted exploitation rate (μ)		1.48	1.07	0.70	0.36	0.21					

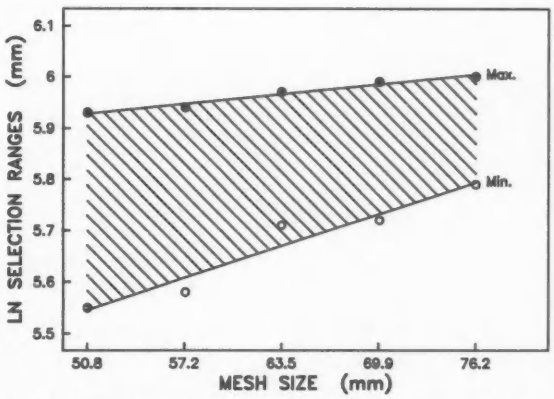

FIG. 8. Relationship between mesh size and selection range (in natural logarithms).

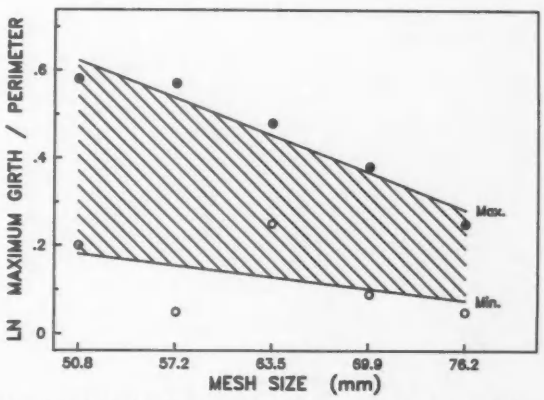

FIG. 9. Relationship between the girth/perimeter ratio (in natural logarithms) and mesh size for the largest and smallest herring caught in each mesh.

mon base of girth–perimeter ratios (Fig. 11). Very few fish were captured when the girth–perimeter ratio was less than 1.0, i.e. herring whose maximum girth is smaller than the net perimeter can swim through the meshes with little hindrance. Suprisingly, there were significant numbers of fish caught whose girth–perimeter ratios were greater than 1.5. However, the small mesh herring nets tended to catch herring of much greater girth–perimeter ratio than the larger nets, regardless of mode of capture (Fig. 12).

The decline in the girth–perimeter ratio with increase in mesh size for the 'wedged' fish in Fig. 12 is consistent with the decrease in compressibility with mesh size observed in Fig. 5. For the other two modes of capture, however, this decline with increase in mesh size is much greater. Compressibility at the snout and gills is therefore likely to be greater and more length–dependent than at the point of maximum body girth.

1986 mesh selectivity experiment

Selectivity curves derived from the 1986 experiment (Fig. 13) are similar to those obtained in 1987 in that they are multimodal in a progression of escalating modes. However the relative fishing power of the various mesh sizes is much different (Table 4). The optimal net in 1986 was the 63.5 mm compared with the 50.8 mm in 1987. In addition, the smaller nets were much less efficient and the larger nets much more efficient in 1986 compared with 1987. Further, the selection range in the smaller nets included much smaller fish in 1987 compared with 1986. Taken together, these observations imply that girths for the same length of herring were greater in 1987 than in 1986. Girth data were not available for 1986 but because girth and weight are directly proportional (Farran 1936), differences in condition factor (i.e. weight $\times$ 1000/L^3) could explain the lower selection range and higher selectivities of the smaller nets

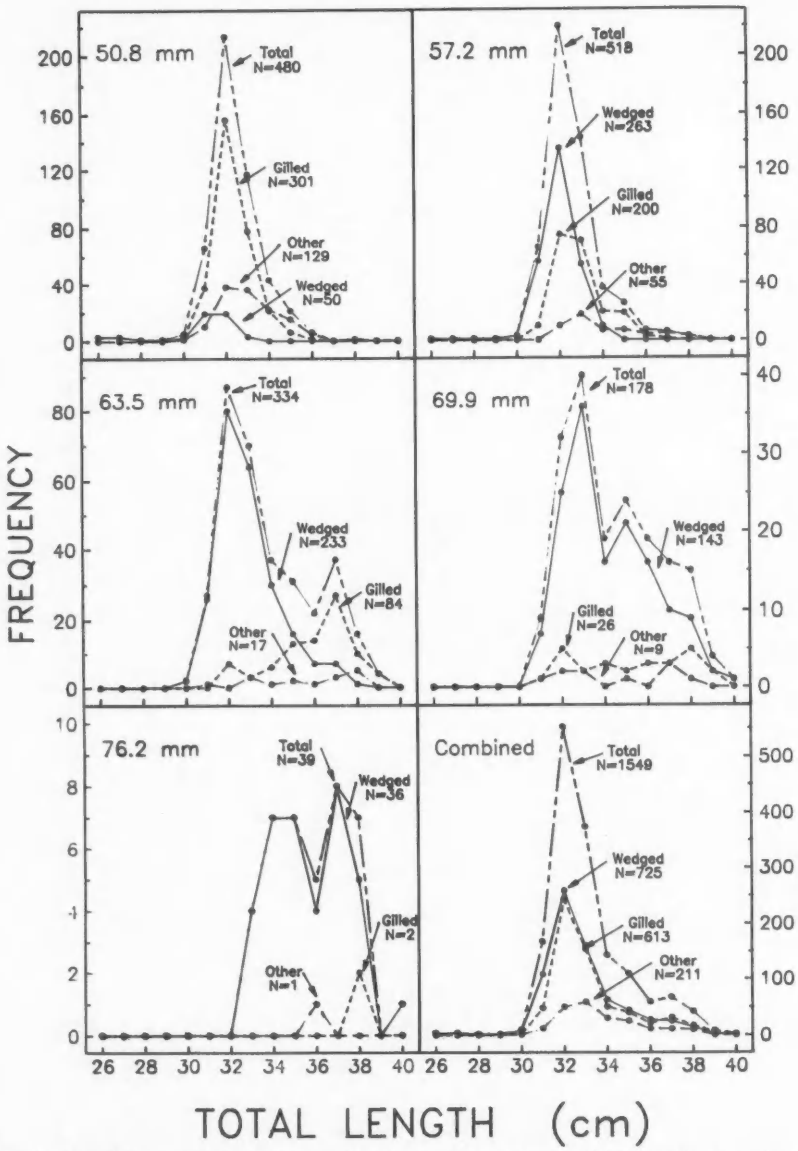

FIG. 10. Length frequencies by mesh size of herring caught by gillnets in 1987 according to mode of capture.

in 1987. Condition factors at length (Fig. 14) were in fact higher in 1987 than in 1986, particularly for lengths less than 32 cm.

These data demonstrate that inter-annual differences in condition factor can have a significant impact on gillnet selectivity of herring. Because fish condition affects its girth at the abdomen more than at the head (Farran 1936: Ishida 1969), small changes in plumpness will also affect the proportion of fish caught by the various modes of capture for each mesh size. This will not only alter the length composition of the catches for a particular mesh size, but will also change the relative fishing power of the different mesh sizes.

Towards a More Reliable Gillnet Selectivity Curve

Most experiments on selectivity are based on fish length because of its ease and frequency of sampling. However, because of the sensitivity of gillnet selectivity of herring to changes in condition factor, girth rather than length should be the critical selection variable. A corollary of this observation is that fish of the same girth to net perimeter ratio should have the same selectivity regardless of mesh size. A composite plot of gillnet selectivities in relation to girth–perimeter ratios (all meshes) (Fig. 15) clearly demonstrates that herring of the same girth–perimeter ratio have highly variable selectivities that are different for different mesh sizes. We have shown this to be due

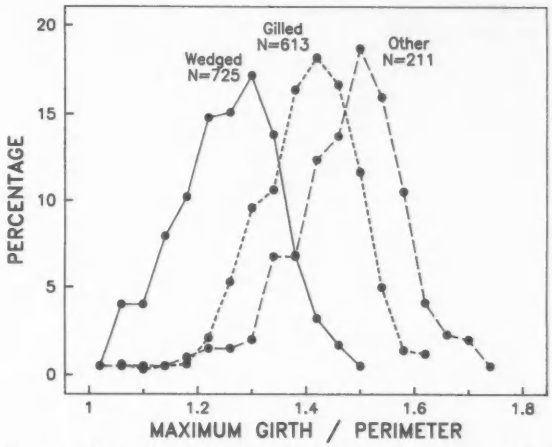

FIG. 11. Distribution of girth/perimeter ratios of herring according to mode of capture (all mesh sizes combined).

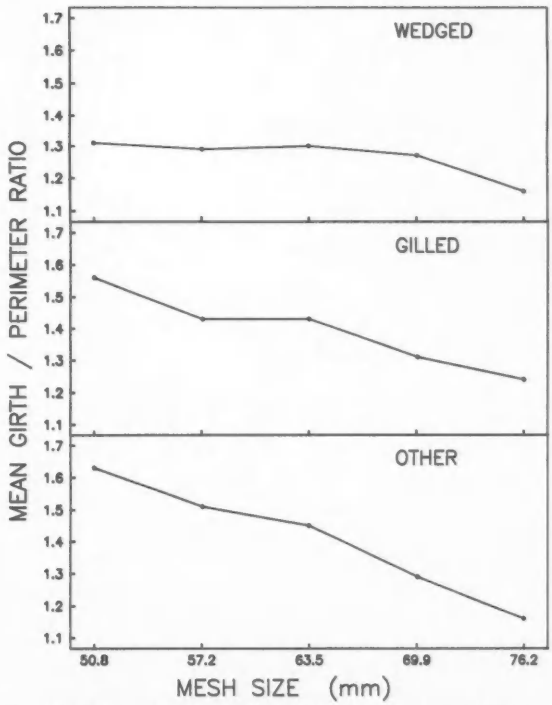

FIG. 12. Changes in the mean girth/perimeter ratio with mode of capture and mesh size of the gillnet.

to the changes in body taper and associated effects on compressibility with increases in body size. Therefore a gillnet selectivity curve for herring must be net-specific and expressed as a function of girth–perimeter ratios. Such data are available for the 1987 experiment. To these data we have fitted a smoothing curve for each mesh size using MacDonald and Green (1985) modal analyses (Fig. 16 and Table 5). Superimposed on these plots is the girth-converted equivalent of the Holt selectivity model. It is obvious from the distribution ranges of the sam-

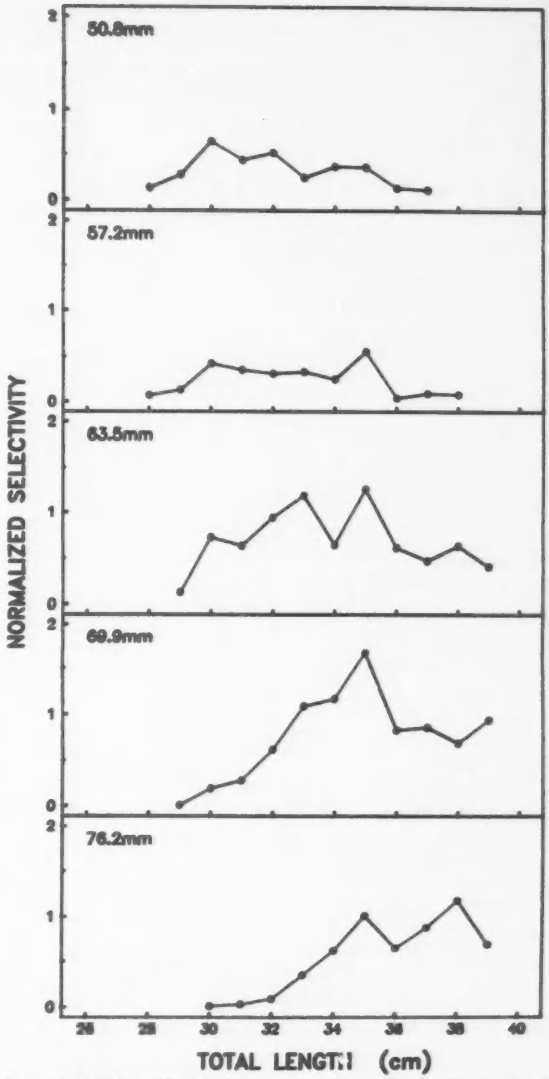

FIG. 13. Mesh-specific selection curves estimated by the direct method for 1986 gillnet samples.

pling data alone that the indirect approach such as illustrated by the Holt model represents a gross distortion of the actual selectivity curve, particularly for the smaller mesh sizes.

Discussion and Conclusion

Our analyses of gillnet selectivities of Atlantic herring have shown that, when estimated directly, the empirical selectivity curves do not adhere to the assumptions of congruency underlying the indirect classical models of Baranov (1948) and Holt (1963). Nor is there any validity in the assumption of equal fishing power between nets of different mesh sizes. Rather, such selectivity curves are multimodal, when expressed as a function of length, with nets of different mesh sizes having variable fishing power. The published literature on gillnet selectivity sup-

TABLE 4. Length-specific exploitation rates (i.e. selectivity rate) of herring estimated directly from the 1986 gillnet data. The adjusted exploitation rate takes into account differences in net area.

Length (cm)	Population l/f ($\times 10^{-5}$)	Exploitation rate ($=\mu \times 10^{-5}$) by mesh size (mm)					Normalized selectivity ($\mu/\bar{\mu}$)				
		50.8	57.2	63.5	69.9	76.2	50.8	57.2	63.5	69.9	76.2
25	1.69										
26	1.00										
27	3.07										
28	6.51	0.15	0.10				0.13	0.07			
29	25.05	0.32	0.19	0.19	0.02		0.27	0.13	0.13	0.01	
30	42.10	0.76	0.60	1.02	0.27	0.02	0.64	0.42	0.72	0.19	0.01
31	63.06	0.51	0.50	0.89	0.39	0.04	0.43	0.35	0.63	0.28	0.03
32	19.83	0.61	0.44	1.33	0.88	0.13	0.51	0.31	0.94	0.62	0.09
33	14.23	0.28	0.47	1.68	1.54	0.49	0.24	0.33	1.19	1.09	0.35
34	25.65	0.43	0.36	0.91	1.66	0.88	0.36	0.25	0.64	1.17	0.62
35	9.44	0.42	0.78	1.78	2.37	1.43	0.35	0.55	1.26	1.67	1.01
36	13.07	0.15	0.05	0.87	1.17	0.92	0.13	0.04	0.61	0.83	0.65
37	15.28	0.13	0.13	0.67	1.22	1.24	0.11	0.09	0.47	0.86	0.88
38	10.75		0.12	0.89	0.97	1.67		0.08	0.63	0.69	1.18
39	2.05			0.58	1.33	0.98			0.41	0.94	0.69
40	0.25					8.00					(5.65)
No. caught		108	147	379	344	204					
Adjusted exploitation rate (μ)		0.46	0.40	0.95	0.78	0.48					

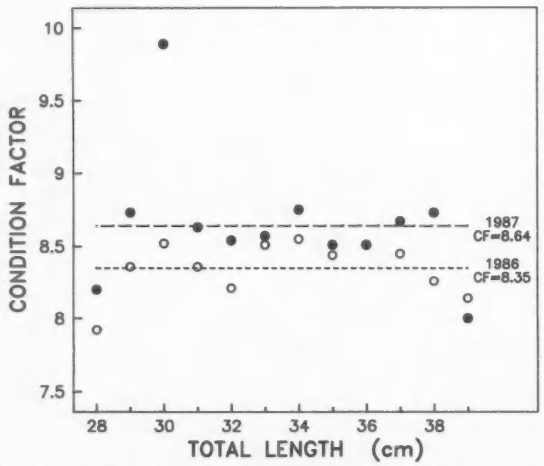

FIG. 14. Condition factor (weight/length^3) of herring plotted against length for 1986 and 1987.

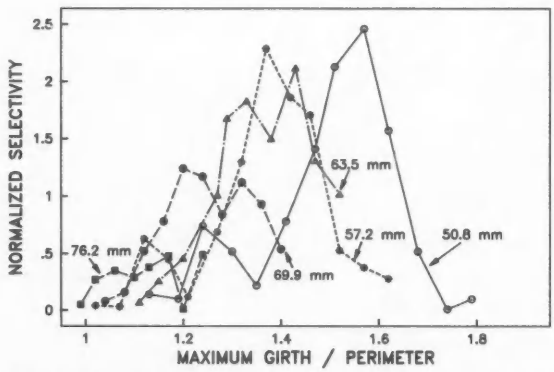

FIG. 15. Composite plot of normalized selectivity estimates for 1987 in relation to girth/perimeter ratios (all meshes combined).

ports this conclusion. Ricker (1949), for example, observed that the youngest fish, which are the most abundant in the population, are not the most abundant when nets of several mesh sizes are fished together. Hamley and Regier (1973) fished a known population of marked walleye with nets of various sizes and found the resulting selectivity curves to be multimodal with amplitudes increasing with mesh size. Similar results were found by Lambou (1961) for gizzard shad, Tester (1935) for Pacific herring, and Trent and Hassler (1968) for striped bass. It is for these reasons that we recommend the direct empirical selectivities (Table 5) as being the most appropriate when interpreting population parameters from herring gillnet catch data.

A critical assumption in our analyses is that the catchability of purse-seine caught fish is independent of length, i.e. length composition of purse seine catches is representative of the population length frequency. There is no obvious way to test this assumption. However, potential biases can be judged on a qualitative basis. These biases could result from two factors viz. selective fishing by the vessel or intrinsic availability differences of fish of different lengths. The first factor can be ruled out since sets were made randomly (as opposed to commercial operations) and each catch was randomly sampled. On the second point, differential distribution by depth of fish of different sizes can occur and is particularly true of 0-group and 1-group herring (Wheeler and Chaulk 1987). However, these young fish are below the selection range of the smallest net used in our selectivity experiments. Further, in many cases entire schools were caught in our research purse-seine sets so that a differential escapement by size is unlikely to be a major bias. We are there-

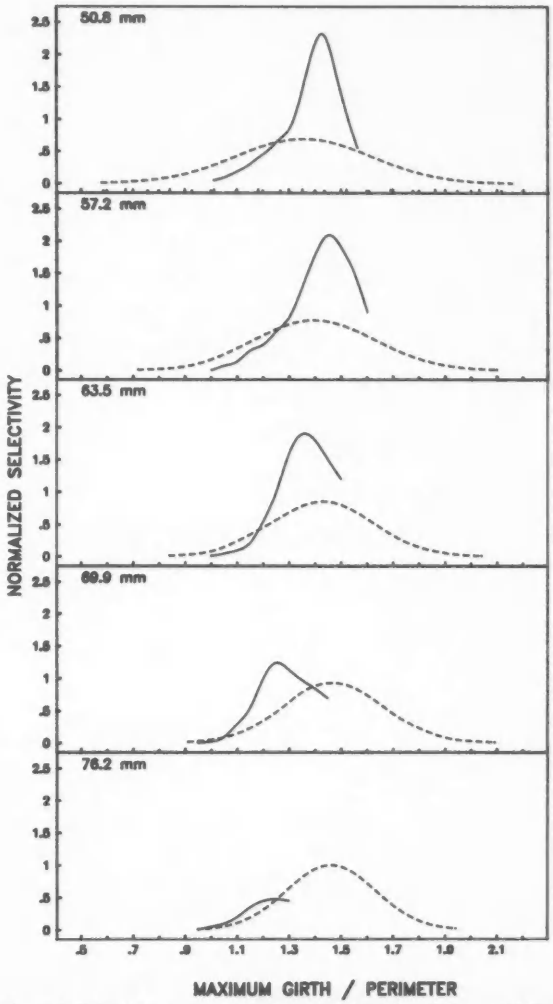

FIG. 16. Selectivity curves, fitted by MacDonald and Green (1985) modal analysis, to the mesh-specific selections estimated by the direct method from the 1987 sampling data (solid lines). Superimposed are the selectivity curves derived from the Holt model (dashed lines).

fore confident that the purse seine length frequencies used in these analyses are relatively unbiased.

Differences in fishing power between nets of different mesh sizes is a primary function of differences in the relative contribution of the various modes of capture to the overall selectivity pattern of particular mesh sizes. These modes of capture have different fishing powers which may vary with mesh size but in general, wedging is more effective than gilling and both modes are much more effective than tangling (i.e. other). Thus, smaller nets tend to capture a greater number of herring which are tangled at the snout, and therefore have a lower fishing power than the larger mesh sizes where wedging is the dominant mode of capture. The decrease in catchability for the larger mesh sizes may be due to larger fish being better able to see the nets since visual acuity improves with age (Hester 1968). We conclude that the selectivity curve of herring for a particular mesh size

TABLE 5. Smoothed selectivity estimates in relation to the girth/perimeter ratio as calculated by the MacDonald and Green (1985) model analysis for the 1987 gillnet data.

Girth/ perimeter	Normalized selectivity by mesh size (mm)				
	50.8	57.2	63.5	69.9	76.2
0.95				.01	.01
1.00		.01	.01	.03	.05
1.05		.08	.05	.07	.10
1.10	0.05	.15	.10	.30	.20
1.15	0.10	.36	.32	.56	.35
1.20	0.18	.40	.55	1.00	.45
1.25	0.27	.60	1.00	1.25	.48
1.30	0.40	.83	1.60	1.10	.45
1.35	0.53	1.30	1.90	1.50	
1.40	0.70	1.80	1.80	0.85	
1.45	0.90	2.10	1.60	0.70	
1.50	1.45	1.90	1.20		
1.55	2.10	0.90			
1.60	2.30				
1.65	1.75				
1.70	1.10				
1.75	0.55				

is unlikely to be unique because of the above-mentioned factors. It can, however, be reasonably approximated when girth is chosen as the critical selection variable. Because lengths are routinely collected during normal sampling of commercial herring catches, conversion of lengths to girths will require length–girth keys specific to stock, season, and year. Finally, because several Northwest Atlantic herring stocks are currently assessed using commercial gillnet catch rates, it is important to document changes in mesh size over time in order to adjust for differences in fishing power.

Acknowledgments

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Experimental Mesocosm Study of the Separate and Interaction Effects of Phosphorus and Mosquitofish (*Gambusia affinis*) on Plankton Community Structure

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Lancaster, H. F., and R. W. Drenner. 1990. Experimental mesocosm study of the separate and interaction effects of phosphorus and mosquitofish (*Gambusia affinis*) on plankton community structure. Can. J. Fish. Aquat. Sci. 47: 471–479.

We examined community impacts of phosphorus and mosquitofish (*Gambusia affinis*) in an experimental mesocosm study of factorial design in which two levels of phosphorus addition were cross-classified with two levels of fish. Total phosphorus (TP), chlorophyll, cryptomonads, unicellular green algae, unicellular blue-green algae, colonial blue-green algae, filamentous blue-green algae, chironomid tube length, cladocerans, fish density, and fish biomass were significantly enhanced in the presence of phosphorus addition. Total nitrogen (TN), TN:TP ratio, Secchi depth, chrysophytes, and periphytic diatoms were suppressed in the presence of phosphorus addition. Diatoms, filamentous blue-green algae, chrysophytes, periphytic unicellular and colonial green algae, periphytic filamentous blue-green algae, and rotifers were enhanced in the presence of mosquitofish. Secchi depth, TN:TP ratio, cyclopoid copepodids, nauplii, cladocerans, and chironomid tubes were suppressed in the presence of mosquitofish. We found significant phosphorus × mosquitofish interaction effects for TN:TP ratio, chrysophytes, dinoflagellates, periphytic colonial green algae, cladocerans, and chironomid tubes. These results show that nutrients and fish do not act as independent regulators of plankton communities but instead have effects which can only be predicted from an understanding of their combined impacts.

Nous avons examiné les effets sur des communautés du phosphore et de la présence de la gambusie (*Gambusia affinis*) au cours d'une étude en mésocosme selon un plan d'expérience factoriel qui comprenait deux niveaux d'addition du phosphore et deux niveaux de populations de poissons. Lorsque du phosphore était ajouté, on a remarqué une augmentation significative du phosphore total (PT), de la chlorophylle, des cryptophycées, des algues vertes unicellulaires, des algues bleues unicellulaires, des algues bleues coloniales, des algues bleues filamenteuses, de la longueur du tube des chironomidés, des cladocères, de la densité des poissons ainsi que de la biomasse des poissons. Lorsque du phosphore était ajouté, l'azote total (NT), le rapport NT:PT, la limpidité de l'eau (disque de Secchi), les chrysophytes et les diatomées périphytes ont été supprimés. En présence de la gambusie, on a observé une augmentation des diatomés, des algues bleues filamenteuses, des chrysophytes, des algues vertes périphytes unicellulaires et coloniales, des algues bleues filamenteuses périphytes et des rotifères. En présence de la gambusie, la limpidité de l'eau (disque de Secchi), le rapport NT:PT, les cyclopidés, les nauplius, les cladocères ainsi que les tubes de chironomidés ont été supprimés. Nous avons trouvé qu'il existe des effets interactifs significatifs entre le phosphore et la gambusie dans le cas du rapport NT:PT, des chrysophytes, des dinoflagellées, des algues vertes coloniales périphytes, des cladocères et des tubes de chironomidés. Ces résultats montrent que les matières nutritives et que les poissons ne constituent pas des régulateurs des communautés planctoniques qui sont indépendants les uns des autres, mais qu'ils ont plutôt des effets prévisibles seulement lorsqu'on a établi leurs effets combinés.

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Plankton communities of lakes are regulated, in part, by both the effects of nutrients and the effects of planktivorous fish. Nutrient concentration, especially phosphorus, is one factor that can determine the biomass of phytoplankton and zooplankton (McQueen et al. 1986). The amount of phosphorus relative to other nutrients also affects phytoplankton species composition (Stoermer et al. 1978; Smith 1982; 1983; Suttle and Harrison 1988). Another factor affecting plankton communities is predation by planktivorous fish. Visually feeding planktivorous fish selectively consume large zooplankton and may enhance small zooplankton and phytoplankton (Lazzaro 1987; Northcote 1988).

This paper presents an outdoor mesocosm experiment of factorial design examining the separate and interaction effects of phosphorus and planktivorous fish as regulators of lentic community structure. Nutrient × fish interactions are effects attributable to the combination of nutrients and fish beyond those which can be predicted from the separate effects of nutrients and fish (Winer 1971). Nutrient × fish interactions have only been examined in a few experiments (Lynch and Shapiro 1981; Vanni 1987a,b; Mazumder et al. 1988; Drenner et al. 1989).

Methods

The experiment was conducted at the Texas Christian University mesocosm facility which consisted of 18 white fiberglass tanks, 2.2 m high, 1.8 m in diameter, containing 5500 L. The tanks were arranged in three rows of six tanks and sampled

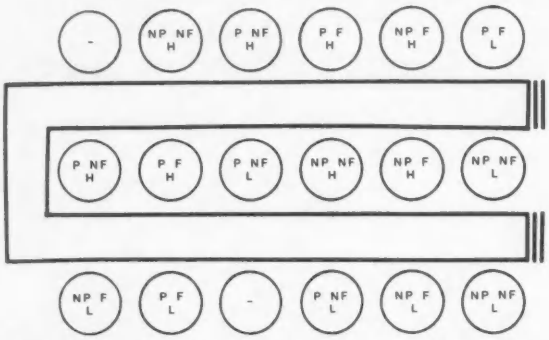

FIG. 1. Layout of the experimental tanks and sampling walkway. Assigned treatment combinations and randomized blocks are shown by the column of letters in each tank (P, NP = phosphorus addition, no phosphorus addition; F, NF = fish present, no fish present; H, L = high TN:TP ratio block, low TN:TP ratio block). Dashes indicate tanks not included in the experiment.

from walkways between the tanks (Fig. 1). To prevent stratification, tanks were mixed for 1 h each day with an airlift mixer system (Drenner et al. 1986).

The water source for the tanks was a small (0.7 ha), shallow (2.5 m maximum depth) pond adjacent to the mesocosm facility. The pond has a fish community consisting of bluegill (*Lepomis macrochirus*) and mosquitofish (*Gambusia affinis*). Water was pumped into the tanks on 28 May using a gasoline powered diaphragm pump. The water intake was positioned 5 m offshore in a plastic can with openings covered with fiberglass screening to exclude fish. Because it rained and changed the water quality of the pond during the day of tank filling, water chemistry samples were collected on 3 June to assess the range of starting nutrient levels in the tanks. Samples for total nitrogen (TN) were digested with alkaline potassium persulfate (D'Elia et al. 1977) and analyzed using the UV absorption method (APHA 1985). Samples for total phosphorus (TP) were digested with potassium persulfate (Menzel and Corwin 1965) and analyzed using the malachite green method (Van Veldhoven and Mannaerts 1987). For the assignment of treatment combinations, the tanks were grouped into two blocks of eight according to high (>30) and low (<30) TN:TP ratios on the day of filling.

The experimental design of the study, a 2 × 2 factorial design (with and without phosphorus addition × with and without fish present), resulted in four treatment combinations: (1) no phosphorus addition and fishless, (2) no phosphorus addition and fish present, (3) phosphorus addition and fishless, (4) phosphorus addition and fish present. Each treatment combination had two replicates in each block of eight tanks, resulting in a total of 16 tanks. The treatment combinations were randomly assigned to tanks within the blocks with the stipulation that the same treatment combinations could not be adjacent within a row (Fig. 1). Because zooplankton occur in low densities near the shore where the water was pumped, we supplemented the plankton communities in the tanks with plankton collected on 4 June in the deepest area of the pond by 16 2-m vertical tows, using an 80-μm mesh conical plankton net. The net tows were combined and distributed in equal aliquots to each of the tanks.

After adding zooplankton on 4 June, the tanks were sampled and the phosphorus and fish were added. Treatment combinations with phosphorus addition received 60 μg P/L in the form of H_3PO_4 which was dissolved in water and mixed in the tanks with a paddle. A similar amount of phosphorus was added on 18 June, midway through the 4-wk experiment. This phosphorus addition was approximately double the epilimnetic total phosphorus concentrations (approximately 30 μg P/L) which occur in the pond in spring (R. W. Drenner, unpubl. data). We used mosquitofish, a live-bearer that feeds as a size-selective zooplanktivore (Bence and Murdoch 1986). Mosquitofish were dip-netted from the pond, and each tank was stocked with 10 small fish (2–3 cm total length (TL)) and 10 large fish (4–5 cm TL), including pregnant females. Based on a subsample of fish, we estimated initial fish biomass to be 3.4 g/m^3 wet weight.

Tanks were monitored at 3–4-d intervals for 4 wk resulting in a total of nine sampling dates. Integrated water column samples for analysis of TP, TN, chlorophyll, and phytoplankton were collected with a PVC tube lowered to near the tank bottom and closed with a valve at the bottom. Water samples on all sampling dates for TP and TN were placed in plastic ziploc bags, frozen, thawed, and analyzed according to methods previously described. Chlorophyll samples on all dates were filtered through 0.45-μm Whatman glass fiber filters and frozen the same day collected. Chlorophyll was extracted with 90% alkalized acetone according to Wetzel and Likens (1979). Phytoplankton samples were preserved in 1% Lugol's, settled overnight in sedimentation chambers, and analyzed for every other sampling date. Ten fields of view were counted with a Wild inverted microscope at 300×, and the algae were identified to taxonomic or morphological group. Approximately 10 individuals of each phytoplankton group were measured to determine average length and width of the cells.

Zooplankton samples were collected from each tank with a single vertical tow of an 80-μm, 16-cm-diameter Wisconsin plankton net. Samples were preserved in 5% sucrose-formalin and counted with a dissecting microscope for every other sampling date.

Tube-dwelling chironomids and periphyton were sampled on 12 June and 8 July, respectively. Chironomid tubes were counted and measured in situ within two 400-cm^2 areas. These areas were on the south side of the tanks from the surface of the water to a depth of 20 cm. Several larvae were removed from each tank for identification. Periphyton was sampled after the tanks were drained on 6–8 July. A circular area (radius 14 mm) of periphyton on the north side of the tanks was removed with a modified epilithon sampler (Douglas 1958) and preserved in a 6:3:1 (water:ethanol:formalin) fixative. Periphyton was counted by the same method as the phytoplankton.

Mosquitofish were recovered during tank draining. Water was drained from tanks through a fiberglass screen, and fish were removed from the tanks with dip-nets. The remaining water and sediments were vacuumed, and the debris was sorted by hand to recover any remaining fish. Mosquitofish were weighed, measured, and preserved in 10% formalin.

A two-way ANOVA revealed that pretreatment zooplankton and phytoplankton densities were not significantly different, except for cyclopoid copepodids that were higher in tanks which would receive a phosphorus addition ($P = 0.049$). Sampling of tanks produced time series data which were analyzed by a two-way randomized block ANOVA for factors with repeated measures. No data effects or date × treatment interaction effects were considered in this study. Densities of periphyton and chironomid tubes were analyzed using a two-way randomized block ANOVA. The ANOVA assessed main effects, interaction effects, and simple effects; and these analyses were com-

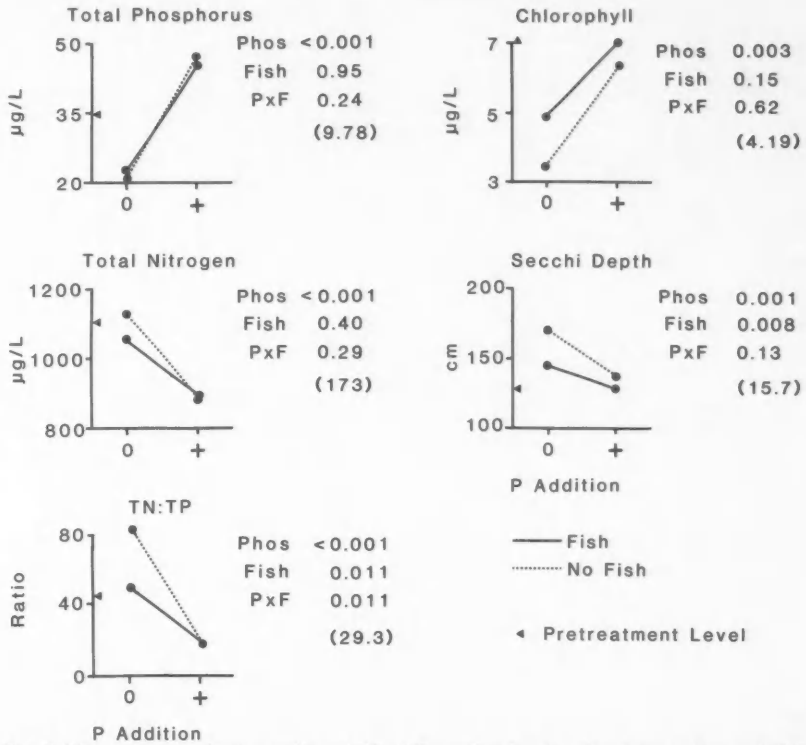

FIG. 2. Mean responses of water quality variables (all sampling dates) to phosphorus and mosquitofish manipulations. Probability values from repeated-measures ANOVA of phosphorus and fish effects and their interaction effects are indicated to the right of each graph. Off-scale initial concentrations are indicated by an upward-pointing arrow. $\sqrt{\text{MSerror}}$ shown in parentheses.

pleted using SAS/STAT version 6 (SAS Institute Inc. 1985). Recovered fish biomass and density were analyzed with a Student's *t*-test. Statistical significance was inferred at $P \leq 0.05$.

Results

Total phosphorus of the water column, chlorophyll, cryptomonads, unicellular blue-green algae, colonial blue-green algae, filamentous blue-green algae, unicellular green algae cladocerans, and chironomid tube length were increased in the presence of phosphorus addition (Figs. 2, 3, 4, and 5). Total nitrogen, TN:TP ratio, Secchi depth, chrysophytes, and periphytic diatoms were decresed in the presence of phosphorus addition (Figs. 2, 3, and 5). Fish reproduction occurred in all tanks and was greatest in tanks with phosphorus addition, as demonstrated by increased fish density and biomass with the added phosphorus (Fig. 6). The higher pre-treatment density of cyclopoid copepodids in tanks with a phosphorus addition was not maintained throughout the experiment. (Fig. 4).

Diatoms, filamentous blue-green algae, chrysophytes, nonpredatory rotifers, periphytic unicellular and colonial green algae, and periphytic filamentous blue-green algae were increased in the presence of fish (Figs. 3, 4, and 5). The ratio of TN:TP, Secchi depth, cyclopoid copepodids, nauplii, cladocerans, and chironomid tubes were suppressed in the presence of fish (Fig. 2, 4, and 5).

The initial differences in TN:TP ratios between high and low TN:TP ratio blocks were not maintained throughout the experiment. However, there was a significant block effect for temperature ($P = 0.003$) due to increased temperature of the tanks in the low TN:TP block predominantly on the south side of the facility. Unicellular green algae were also enhanced in the low TN:TP block ($P = 0.047$).

Significant phosphorus × fish interaction effects were observed for the TN:TP ratio, chrysophytes, dinoflagellates, cladocerans, chironomid tubes, and periphytic colonial green algae (Figs. 2, 3, 4, and 5). The simple effects of phosphorus and fish for the response variables showing significant interaction effects are shown in Table 1. Fish enhanced the density of chrysophytes and dinoflagellates, and suppressed the TN:TP ratio and the density of chironomid tubes only in the treatment combinations without a phosphorus addition. Fish enhanced the density of periphytic colonial green algae only in treatment combinations with a phosphorus addition. Phosphorus addition suppressed the density of chironomid tubes and enhanced the density of dinoflagellates and cladocerans only in treatment combinations without fish. Phosphorus addition suppressed the density of chrysophytes and enhanced the density of periphytic colonial green algae only in the treatment combinations with fish.

Discussion

In this experiment, phytoplankton biomass, cladoceran densities, and mosquitofish biomass and densities were enhanced in

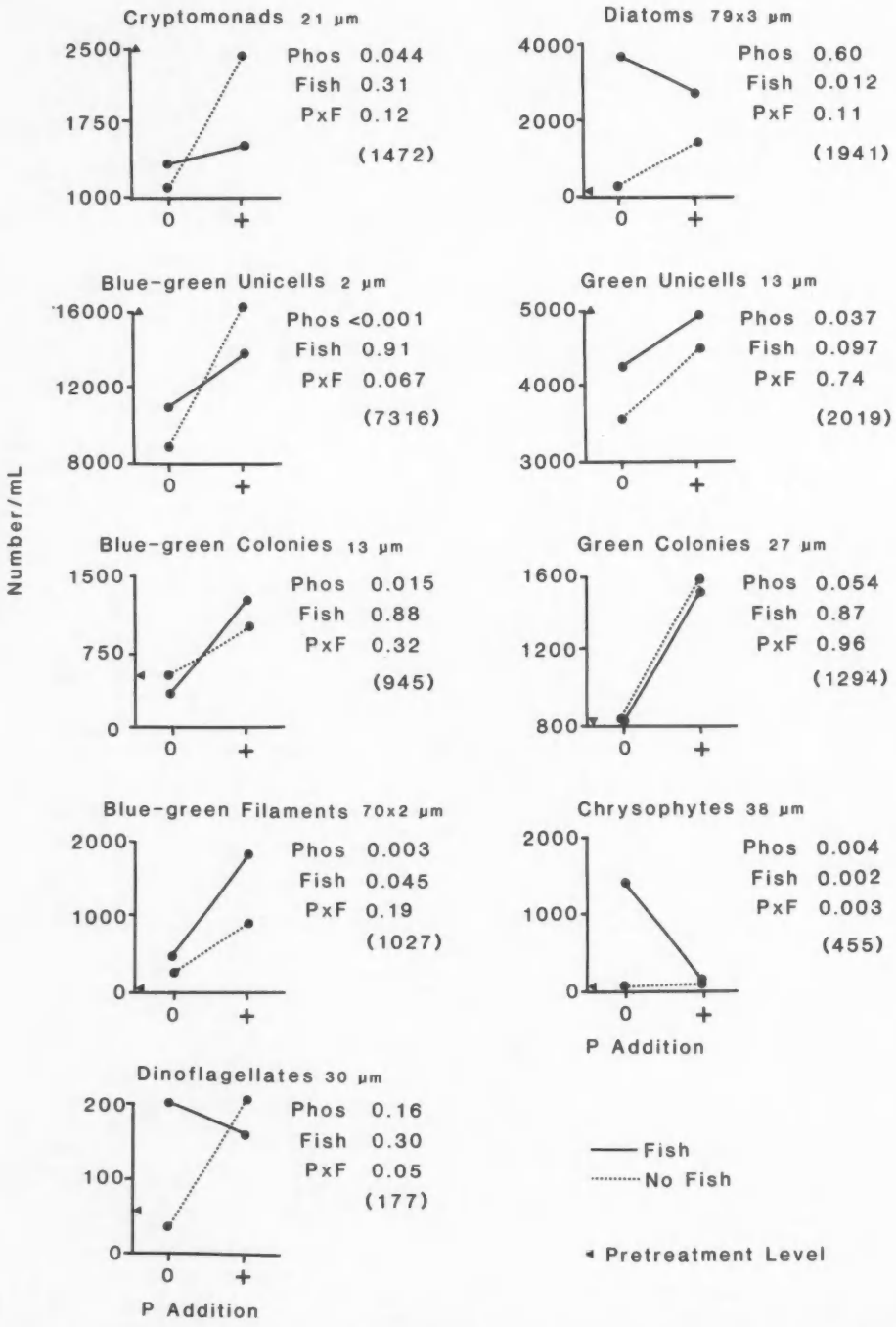

FIG. 3. Mean responses of phytoplankton taxa (all sampling dates) to phosphorus and mosquitofish manipulations. Probability values from repeated-measures ANOVA of phosphorus and fish effects and their interaction effects are indicated to the right of each graph. Off-scale initial densities are indicated by an upward-pointing arrow. $\sqrt{\text{MSerror}}$ shown in parentheses.

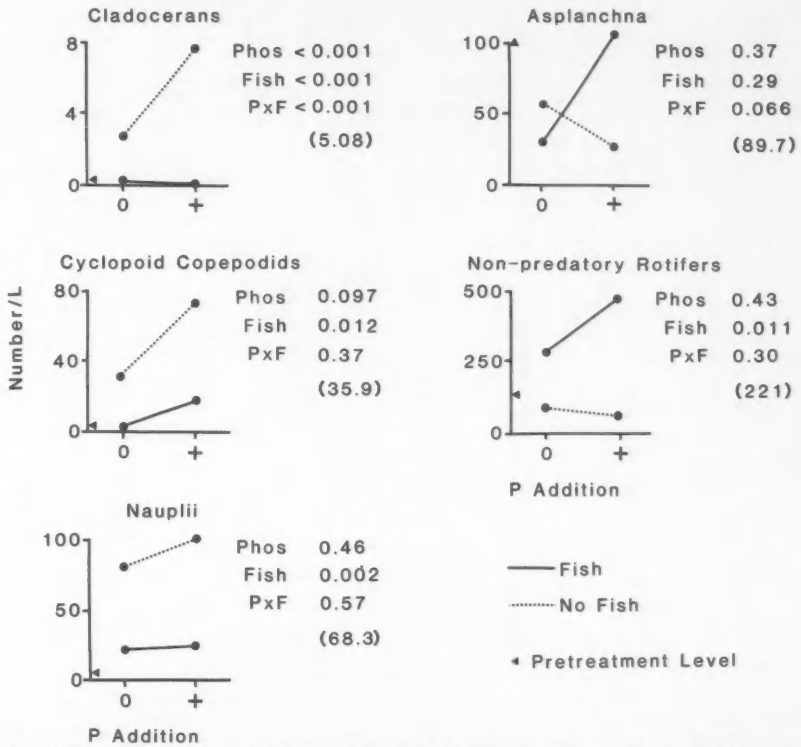

FIG. 4. Mean responses of zooplankton taxa (all sampling dates) to phosphorus and mosquitofish manipulations. Probability values from repeated-measures ANOVA of phosphorus and fish effects and their interaction effects are indicated to the right of each graph. Off-scale starting values are indicated by an upward-pointing arrow. $\sqrt{\text{MSerror}}$ shown in parentheses.

the presence of phosphorus addition, indicating that productivity of the community was, in part, phosphorus limited. Phosphorus addition also altered phytoplankton species composition. Blue-green algae may have increased due to the lowering of the TN:TP ratio from 69.4 without phosphorus addition to 22.2 with phosphorus addition. Blue-green algae tend to be rare in lakes in which the TN:TP ratio exceeds 29:1 but may dominate the phytoplankton community of lakes with a TN:TP ratio less than 29:1 (Smith 1983; but see McQueen and Lean 1987). The chrysophytes, which were principally *Dinobryon*, were suppressed by the phosphorus addition in the presence of fish. Some species of *Dinobryon* have a competitive advantage at low phosphorus levels due to efficient phosphorus uptake (Lehman 1976).

Phosphorus addition also had a significant effect on the attached community in the tanks. Periphytic diatoms were reduced in the presence of the phosphorus addition. According to Tilman et al. (1986), diatoms may dominate communities at high TN:TP ratios but comprise a smaller percentage of the algal community at low TN:TP ratios. Although the dominant diatom species in the periphyton was also the dominant diatom species in the plankton community, planktonic diatoms were not affected by the phosphorus addition. Conversely, the phosphorus addition increased some algal groups such as unicellular, colonial, and filamentous blue-green algae, and unicellular green algae in the plankton but had no effect on these groups in the periphyton. This difference in the response of phytoplankton and periphyton may be caused by only sampling the periphyton on one date while the plankton community was evaluated based on five sampling dates. However, these results may also indicate that algal taxa have different responses to nutrient addition, depending on whether they are members of the plankton or periphyton communities.

The phosphorus addition also increased chironomid tube length and decreased the density of chironomid tubes in the absence of mosquitofish predation pressure. Arruda (1979) found larger and fewer chironomid larvae with increased primary productivity of ponds. He suggested that the change in chironomid size may have been due to either a change in species or a change in size of individuals within a species. In this tank study, the change in chironomid tube size reflected a change in the size of the individual and not a species change because the same chironomid species (*Goeldichironomus holiprasinus*) was dominant in fishless tanks with or without phosphorus addition. The decrease in the density of chironomid tubes with phosphorus addition may have occurred because the chironomids grew faster and emerged more rapidly at the higher nutrient levels (Hall et al. 1970). We observed chironomid emergence during the study but did not collect the exuviae.

Plankton composition of the tanks was also controlled by fish. The presence of mosquitofish was associated with a suppression of large zooplankton and enhancement of nonpredatory rotifers. These mosquitofish impacts are typical of visually feeding fish which feed as size-selective predators on large

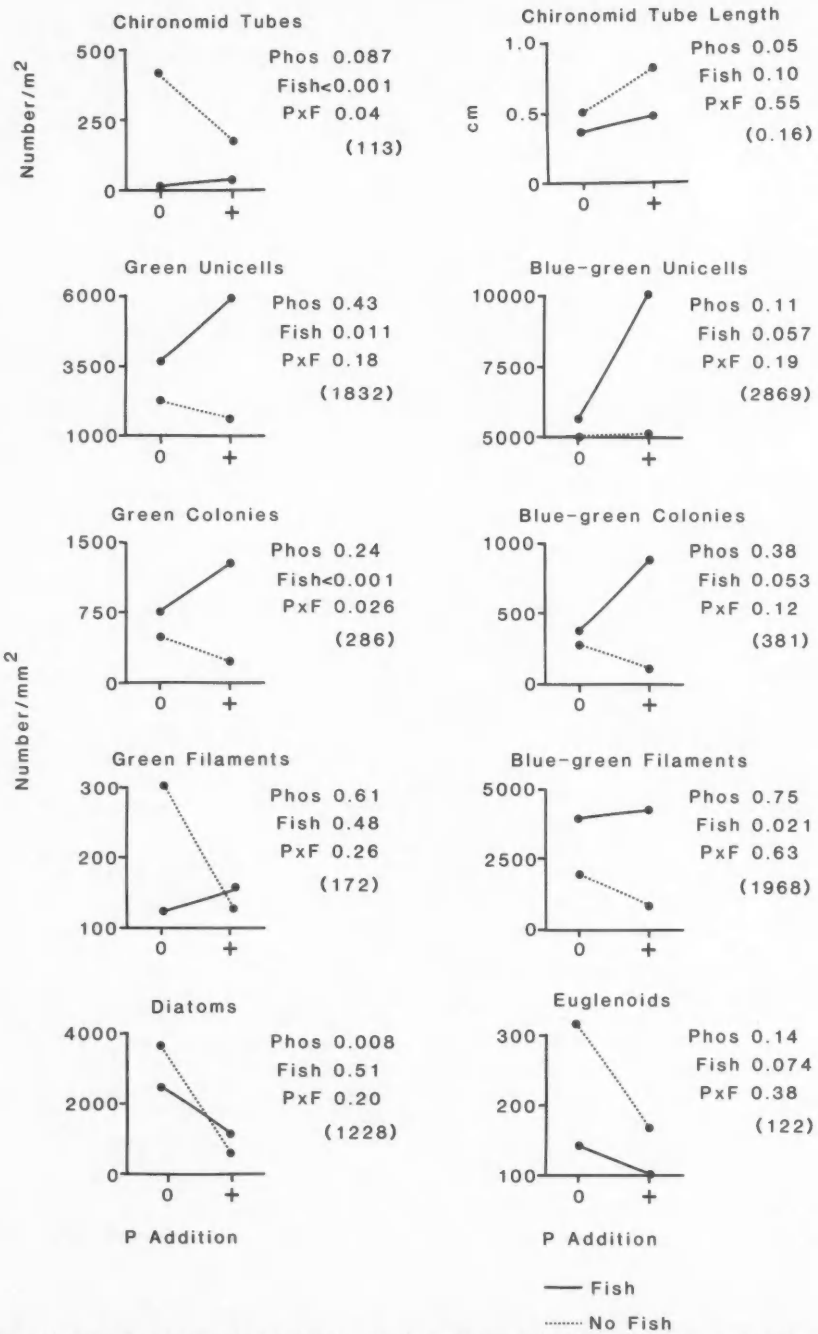

FIG. 5. Mean responses of the attached community (one date) to phosphorus and mosquitofish manipulations. Probability values from ANOVA of phosphorus and fish effects and their interaction effects are indicated to the right of each graph. $\sqrt{\text{MSerror}}$ shown in parentheses.

zooplankton (Lazzaro 1987; Northcote 1988). Previous investigations of mosquitofish impacts in pool and pond experiments have also found that mosquitofish suppressed large zooplankton (Hurlbert et al. 1972; Hurlbert and Mulla 1981). In the pond experiment (Hurlbert and Mulla 1981), mosquitofish enhanced small rotifers, but in the pool study (Hurlbert et al. 1972) rotifers were suppressed after large zooplankton were eliminated.

Hurlbert et al. (1972) and Hurlbert and Mulla (1981) found

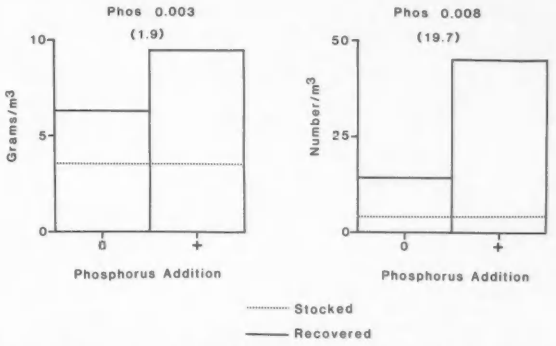

FIG. 6. Mean mosquitofish biomass (wet weight) and density stocked in and recovered from tanks. Probability values from *t*-test evaluating the effect of phosphorus addition are indicated at the top of each graph. SD in parentheses.

TABLE 1. Simple effects of fish and phosphorus for response variables that have significant phosphorus × fish interaction effects. (P, NP = phosphorus addition, no phosphorus addition; F, NF = fish present, no fish present)

	Fish effect		Phosphorus effect	
	Phosphorus absent	Phosphorus added	Fish absent	Fish added
Treatment Combination Comparisons	NP NF versus NP F	P NF versus P F	NP NF versus P NF	NP F versus P F
N:P Ratio	0.001	0.96	<0.001	0.001
Chrysophytes	<0.001	0.75	0.96	<0.001
Dinoflagellates	0.040	0.45	0.024	0.63
Periphytic green colonies	0.16	<0.001	0.37	0.020
Cladocerans	0.002	<0.001	<0.001	0.82
Chironomid tubes	<0.001	0.11	0.013	0.76

TABLE 2. Summary of factorial experiments statistically examining nutrient × fish interaction effects on freshwater communities. NI = no information; – = no significant interaction effect at the level chosen by the author; and * = significant interaction effect. The number in parentheses represents the proportion of the categories with significant interaction effects.

Study	Lynch and Shapiro 1981	Vanni 1987a, 1987b	Vanni 1987a, 1987b	Mazumder et al. 1988	Threlkeld 1988, exp. 4	Threlkeld 1988, exp. 5	Qin 1988	Drenner et al. 1989	This study
Experimental unit	Enclosure	Enclosure	Enclosure	Enclosure	Tank	Tank	Tub	Tank	Tank
Replicates/treatment Comb.	1–2	3	3	2	3	3	2	3	4
Nutrient additions	weekly	weekly	weekly	weekly	once	once	once	once	biweekly
(μg P/L)	10, 30	10	10	6.5	(Dead fish)	(Dead fish)	42	100,200	60
(μg N/L)	110,330	300	300	84.5			250	0	0
Fish species	Bluegill	Bluegill	Bluegill	Yellow perch	Silverside	Silverside	Silverside	Mosquitofish	Mosquitofish
Stocking rate									
(fish/m^3)	0.7	1.0	0.4	0.2	1.1, 4.6	1.1, 4.6	11.1	3.7	3.6
(g/m^3)	NI	NI	NI	0.6 Wet weight	1.0, 4.1 Dry weight	0.9, 3.5 Dry weight	NI	1.4 Wet weight	3.4 Wet weight
Nutrient × fish effects									
Nutrients	*	NI	NI	NI	NI	NI	—	—	*
Water clarity	NI	NI	NI	—	—	—	—	—	—
Bacteria	*	NI	NI	—[b]	NI	NI	NI	NI	NI
Phyto biomass[a]	—	—	—	—	—	*	—	—	—
Phyto categories	* (0.17)	* (0.14)	—	*[c] (0.33)	—	—	—	NI	* (0.22)
Zoop categories	NI	* (0.17)	* (0.42)	—[d]	* (0.67)	—	* (0.80)	* (0.33)	* (0.20)
Insect larvae	NI	NI	NI	NI	NI	NI	NI	NI	*
Periphyton categories	NI	NI	NI	NI	NI	NI	NI	NI	* (0.13)

[a]Lynch and Shapiro (1981) and Vanni (1987a, 1987b) measure biovolume density. Mazumder et al. (1988); Threlkeld (1988); Qin (1988); Drenner et al. (1989); and this study measure chlorophyll levels.
[b]Particulate phosphorus fraction 0.2–1 μm.
[c]Particulate phosphorus fraction 1–3 μm, 3–20 μm, 20–200 μm.
[d]Particulate phosphorus fraction >200 μm.

that mosquitofish presence increased phytoplankton biomass, but we detected no significant effect of mosquitofish on chlorophyll levels in this study. This difference in mosquitofish impact on phytoplankton may be due to differences in zooplankton community structure. Large cladocerans, particularly *Daphnia* greater than 1 mm, are thought to exert the most intense grazing pressure on phytoplankton (Shapiro 1980; McQueen et al. 1986). In Hurlbert et al. (1972), *Daphnia* were present and cladocerans were abundant (133 cladocerans/L in fishless pools), while in Hurlbert and Mulla (1981), cladocerans (*Ceriodaphnia* and *Daphnia*) had a lower density (approximately 10 to 100 cladocerans/L in fishless ponds in the spring). In our study, *Daphnia* were rare and cladocerans were less abundant (2.9 cladocerans/L in fishless tanks without phosphorus addition), although we may have underestimated cladoceran density because the dominant cladoceran, *Simocephalus*, attached to the walls of the tanks.

Mosquitofish may not have significantly affected the phytoplankton in this study because of the low density at which fish were stocked. Fish effects on phytoplankton increase with fish density because higher levels of fish may exert more intense

predation pressure on herbivorous zooplankton and higher levels of fish may release more nutrients due to weight loss or mortality (Threlkeld 1987, 1988). In Hurlbert et al. (1972), the high density at which mosquitofish were stocked (24 g/m^3) may have contributed to the enhancement of phytoplankton. In our mesocosm study, mosquitofish were stocked at lower levels (3.4 g/m^3), and mosquitofish biomass increased (recovered biomass of 6.3 g/m^3 without phosphorus addition and 9.5 g/m^3 with phosphorus addition), suggesting that the mosquitofish incorporated phosphorus and acted as a phosphorus sink (Kitchell et al. 1975).

The effect of fish on the attached community may have masked the effect of fish on phytoplankton. The density of chironomid tubes was suppressed by the presence of fish, although this suppression occurred only in the absence of a phosphorus addition. When released from chironomid grazing, periphytic unicellular and colonial green algae and periphytic filamentous blue-green algae were enhanced. The enhanced periphyton taxa may have competed with the phytoplankton for nutrients and thus prevented mosquitofish from increasing phytoplankton biomass.

While the separate effects of nutrients and fish have received considerable attention, the role of nutrient × fish interaction effects as regulators of plankton communities has been examined in only a few experiments (Lynch and Shapiro 1981; Vanni 1987a,b; Mazumder 1988; Threlkeld 1988; Qin 1988; Drenner et al. 1989) (Table 2). These studies were factorial experiments in which two or more levels of nutrient addition were cross-classified with the presence and absence of visually feeding fish. The experiments differed in respect to the response variables evaluated and experimental design, with nutrient addition and fish treatments varying qualitatively and quantitatively. Significant nutrient × fish interaction effects were found for most kinds of response variables (i.e. nutrients, bacteria, phytoplankton biomass, phytoplankton and zooplankton taxa, insect larvae and periphyton). However, in any given study, only a few response variables showed evidence of nutrient × fish interaction effects. The general trend was for zooplankton to be more affected by nutrient × fish interaction effects than phytoplankton. In the experiments of Qin (1988) and Threlkeld (1988), significant nutrient × fish interaction effects were detected for more than 50% of the zooplankton taxa present in the studies. Although additional research will be necessary to more thoroughly define the limnological conditions under which nutrient × fish interaction effects occur, these experiments suggest that nutrient × fish interactions are important in the regulation of plankton communities.

Acknowledgments

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Lake Dynamics and the Effects of Flooding on Total Phosphorus

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The concentration of total phosphorus in Lake Washington before and after the sewage diversion project was simulated using first-order linear dynamics. Fluctuation in total phosphorus in the lake occurred as a forced response to changes in inflow phosphorus concentration. The dynamics of total phosphorus in Lake Washington was adequately represented by two independent time scales based on water renewal and sedimentation. The water renewal time scale was modelled as a time dependent process. Sedimentation of total phosphorus, on the other hand, appeared constant over the 16-yr period that data were available. A marked increase of total phosphorus in the lake occurred during two flood periods when high concentrations of total phosphorus corresponded to small values of the water renewal time scale (i.e., high flows). At other times, peak concentrations of total phosphorus in the inflow coincided with large values of the water renewal time scale and the lake was dynamically unable to respond to these peaks.

La concentration en phosphore total du lac Washington avant et après la mise en service de la déviation projetée des eaux d'égout, a été simulée selon une dynamique linéaire du premier ordre. Les fluctuations de la concentration en phosphore total dans le lac sont une réponse forcée aux changements de concentration en phosphore dans l'eau d'alimentation. La dynamique du phosphore total dans le lac Washington a été représentée adéquatement grâce à deux échelles chronologiques indépendantes et fondées sur le renouvellement de la masse d'eau et sur la sédimentation. L'échelle de durée de renouvellement de l'eau a été modélisée en fonction du temps. Par ailleurs, la sédimentation du phosphore total paraissait rester constante à l'intérieur de la période de 16-ans pour laquelle les données étaient disponibles. Il s'est produit une augmentation marquée du phosphore total dans le lac à l'occasion de deux crues, alors que les concentrations élevées en phosphore total ont correspondu à des valeurs faibles sur l'échelle chronologique de renouvellement de l'eau (c.-à-d. des débits élevés). À d'autres moments, les concentrations maximales en phosphore total dans l'eau d'alimentation du lac coïncidaient avec les valeurs élevées observées à l'échelle chronologique de renouvellement de l'eau et le lac était incapable, sur le plan dynamique, de répondre à ces pointes.

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Sawyer (1947) observed that when the total phosphorus concentration in a lake was greater than 10 to 20 mg/m^3 algal blooms frequently occurred. The lower limit of Sawyer's observation was used by Vollenweider (1968, 1975, 1976) as the criterion to quantify eutrophication. The problem of predicting the trophic state of a lake is then reduced to one of predicting when the concentration of total phosphorus in a lake, P_L, exceeds 10 mg/m^3 from estimates of phosphorus input to the lake. Towards this end, Vollenweider produced several phosphorus loading models that assume that lakes are in equilibrium with respect to phosphorus. The accuracy of these steady-state models was critically reviewed by Kenney (1982, 1990).

In the present paper the dynamics of total phosphorus in lakes is modelled as a first-order linear system with time dependent coefficients. The model has one source term for phosphorus, the total inflow to the lake. Two sink terms remove phosphorus from the model lake, the outflow from the lake, and sedimentation to the lake bottom. The forced response of the model is calculated using 16 yr of published inflow data from Lake Washington as input. Results are compared with the measured response of Lake Washington following sewage diversion from the lake. Two flood years had a marked effect on the total phosphorus concentrations in Lake Washington.

Lake Phosphorus Dynamics

A Well Mixed Lake with Two Time Scales

Consider a well-mixed lake with a single inflow and a single outflow. Let Q be the volume flow of water into the lake at any time t and assume the lake level is constant with a mean depth z. The surface area of the lake is A and the lake concentration of total phosphorus is P_L. The concentration of phosphorus in the inflowing water is P_i and in the outflowing water is P_L (because the lake is assumed well-mixed). Consider that total phosphorus may also be removed from the lake by sedimentation. Here the assumption is made that the rate of removal by sedimentation is proportional to the concentration of phosphorus in the lake, P_L, and the proportionality constant will be called σ. An alternative suggestion of Edmondson and Lehman (1981) that phosphorus sedimentation in lakes is proportional to phosphorus inflow was refuted by Kenney (1990).

Step Function Response

The step function response describes the increase in lake concentration of phosphorus with time after the sudden start of

phosphorus addition at the inflow. Using similar techniques a sudden decrease can also be calculated. The step function response is important because it permits a ready determination of the time scales or the frequency response characteristics of total phosphorus in a lake.

Here the problem is to determine P_L at any time t after the continuous introduction of phosphorus at the inflow, P_i, beginning suddenly at time $t=0$. The assumption can be made, without loss of generality, that the initial lake concentration was zero at time $t=0$.

If the problem was to be approached from an experimental point of view the first task would be to perform a dimensional analysis of the independent variables, P_i, P_L, Q, A, z, t, and σ. Three dimensionless groups may be found, either by inspection or by using the Buckingham Π theorem (Taylor 1974), as

$$(1)\quad \frac{P_L}{P_i} = \text{Func}\left(\frac{Qt}{Az}, \sigma t\right).$$

Equation (1) states that the dimensionless concentration P_L/P_i is some unknown function of the two dimensionless variables Qt/Az and σt. The actual functional relationship depends upon equations governing the process. Using the empirical approach, the unknown function would be determined by the experiment — by correlating P_L/P_i against Qt/Az and σt, for example. This task could become formidable if the unknown function is nonlinear.

In this simple case, it is not necessary to conduct a series of experiments to determine the unknown function. The equation governing total phosphorus for the model lake can be written directly, using the principle of conservation of mass as,

$$(2)\quad \frac{dP_L}{dt} = \underset{\text{(source)}}{\frac{P_i Q}{Az}} - \underset{\text{(sink)}}{\frac{Q P_L}{Az}} - \underset{\text{(sink)}}{\sigma P_L}$$

This equation has one source term and two sink terms. The rate of change of phosphorus in the lake, dP_L/dt, is equal to the difference between the rate at which the concentration is increasing because of phosphorus in the inflow and the rate at which the concentration is decreasing because of losses to the outflow and sedimentation.

Equation (2) is a first order ordinary differential equation that can be readily solved by separation of variables. The solution, subject to the initial conditions, $P_L=0$ at $t=0$, is:

$$(3)\quad \frac{P_L}{P_i} = \frac{1}{1+\frac{Az\sigma}{Q}}\left(1 - \exp(-Qt/Az)\exp(-\sigma t)\right).$$

Thus, the unknown function in equation (1) has been found for the 'model' lake. If the governing equation was different due to a different set of initial assumptions (say, about mixing), then this unknown function would also be different.

The form of the solution (i.e. the step function response in equation (3)) is shown in Fig. 1 for several different lakes. In each case, the concentration of total phosphorus in the lake increases rapidly following the step increase in the inflow concentration at time zero and eventually reaches an asymptotic value at steady-state.

The term Az/Q is one time scale, τ_w, controlling the dynamics of total phosphorus in lakes. It is known as the water renewal time or water residence time. The second time scale, $\tau_s = 1/\sigma$, will be called the sedimentation time scale. Because of the form

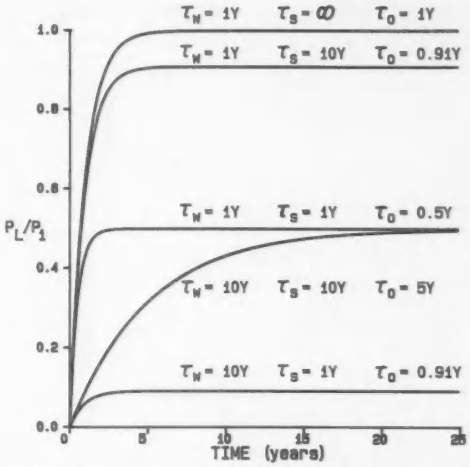

FIG. 1. Step function response of total phosphorus in lakes with two time scales: τ_w, the water renewal time scale and τ_s, the sedimentation time scale. The overall time scale, τ_o, is also given for each lake. Note that a time of $5\tau_o$ is required to reach 99% of the steady-state value.

of the solution for this model an overall time scale, τ_o, can also be determined as,

$$(4)\quad \tau_0 = \frac{1}{\frac{1}{\tau_w}+\frac{1}{\tau_s}} = \frac{\tau_w}{1+\frac{\tau_w}{\tau_s}}$$

The overall time scale for lake phosphorus is always less than the water renewal time for any finite value of sedimentation.

In the steady-state,

$$(5)\quad \frac{P_L}{P_i} = \frac{1}{1+\frac{Az\sigma}{Q}} = \frac{1}{1+\frac{\tau_w}{\tau_s}} \cdot (t \to \infty)$$

At steady-state, the total phosphorus concentration in a lake with no sedimentation is equal to the inflow concentration (i.e. $P_L = P_i$ for $\tau_s \to \infty$). To reach a reasonable estimate of the final steady-state value (say 99%) requires a time of $t=5\tau_w$ (or $5\tau_o$). For all values of $t<5\tau_w$, $P_L<P_i$.

With sedimentation, the steady-state lake concentration is always less than the inflow concentration. The steady-state value of P_L depends not only on water renewal but also on the sedimentation time scale. Therefore, two vastly different lakes (one with a high flushing rate and a high sedimentation rate and the second with low flushing and low sedimentation) can have the same steady-state value of lake concentration (Fig. 1). The time required to reach steady-state, however, is much longer in the latter case. In general, the higher the flushing rate (i.e. the smaller τ_w) for a given sedimentation rate, the closer the steady-state value of P_L will be to P_i. Conversely, the higher the sedimentation (i.e. the smaller τ_s) for a given flushing rate, the smaller the final value of P_L. As before, 99% of the steady-state value is reached in a time equal to $5\tau_o$.

Forced Response

Monitoring lake concentrations after a sudden change in input is a useful method to determine the dynamics of lake phospho-

rus. For very small lakes, this approach is possible empirically by conducting 'whole lake experiments.' For most lakes, however, experimental manipulation is not practical. In general, the phosphorus input is neither constant nor subject to sudden changes. Rather, it is continuously changing. The lake concentration is also constantly changing in an attempt to follow the input concentration. How closely the lake concentration follows the changes in inflow concentration (or forcing) depends upon the lake phosphorus dynamics (i.e. τ_w,τ_s, or τ_o). For forcing frequencies that are small compared with τ_o^{-1}, the lake concentration follows the forcing exactly. For forcing frequencies that are high compared with τ_o^{-1}, the lake concentration shows little or no response to changing inflow concentrations.

Equation (2) has been rewritten to explicitly show the time dependent forcing by P_i as,

$$(6)\quad \tau_w(t)\frac{dP_L(t)}{dt} + \{1 + \sigma(t)\tau_w(t)\}\,P_L(t) = P_i(t).$$

Equation (6) also has time dependent coefficients for both τ_w and σ. It was implicitly assumed earlier that these coefficients were constants. Most temperate lakes, however, are subjected to large variations in flow (Q) throughout the year, with peak flows usually occurring during spring runoff. Changes in lake level (z) and volume (Az) may also be large, particularly for lakes used for hydroelectric purposes. These variables directly affect the water renewal time scale, making τ_w time dependent.

The factors that affect σ are not as well understood. It is known that physical sedimentation is a nonstationary random process that can be positive or negative at various times. A negative sedimentation flux (i.e. resuspension) occurs to some extent in the water column of all lakes and is very common in shallow lakes. Because physical sedimentation is controlled principally by the level of turbulence in a lake seasonal variations in σ are possible, reflecting differences between turbulence under winter ice and during open water in temperate lakes. Biological processes may also play an important role in sedimentation of total phosphorus by controlling the rate of particle generation in the water column.

Temporal variations in the coefficients may be more important than variations in the phosphorus concentration of the inflow (forcing) for many lakes. In very complicated lakes, the forcing and the time dependent coefficients may be coupled; say, by the flow through the lake, Q. Before discussion of a specific numerical example, it may be stated in general that a large spring runoff tends to make the spring lake phosphorus concentration equal to the spring inflow concentration by greatly reducing the instantaneous value of τ_w (and τ_o).

Before equation (6) can be solved, the temporal variation in τ_w and σ must be known (or independently 'predicted') either in the form of time histories for random variations or in the form of analytical functions for periodic variations. The model forcing must also be input to the model. For a hindcast, $P_i(t)$ is usually input as time histories of measured phosphorus inflow to a lake. Anticipated changes in phosphorus inflow, however, may also be input to the model (either as a time series or as an analytical function) in order to forecast future lake changes.

Phosphorus Dynamics in Lake Washington

Input Data

Edmondson and Lehman (1981) published an excellent set of data tracing the recovery of Lake Washington following diversion of sewage from the lake. These data represent as close an approximation to step function forcing as one could expect for such a large lake. Annual mean values of total phosphorus in the inflow to the lake were presented for the period 1962 to 1978 and monthly mean data were given from 1970 to 1978. Instantaneous values of the concentration of total phosphorus in the lake were also presented as determined on January 1 each year from 1962 to 1978. The lake concentration data were spatial averages from an unspecified number of locations.

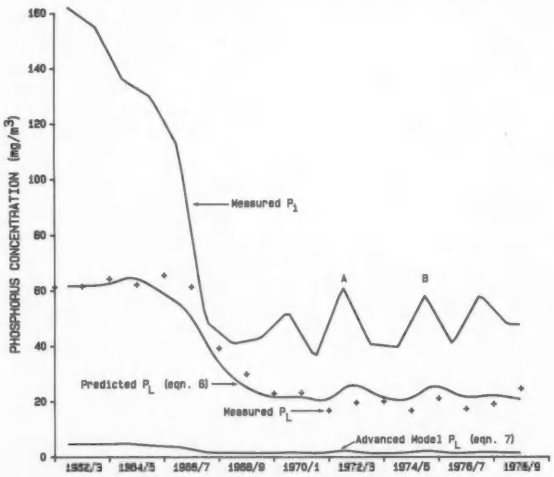

FIG. 2. Simulated responses of P_L, the concentration of total phosphorus in Lake Washington, produced by P_i, the annual mean values of the phosphorus inflow measured from 1962 to 1978. The instantaneous lake concentration of total phosphorus measured on January 1 of each year are also shown.

Total phosphorus concentrations in Lake Washington were simulated using equation (6) as the phosphorus dynamics model. Integration was performed with a variable step, fourth order, Runge-Kutta routine with a base time of 1 d.

Daily inputs to the model $P_i(t)$ and $\tau_w(t)$ were linearly interpolated from the published data. No sedimentation data were given in Edmondson and Lehman (1981) that would permit one to determine the sedimentation time scale as a function of time. A value for τ_s was calculated using equation (5) assuming that Lake Washington was approximately in equilibrium at the beginning of the available data set. In effect, τ_s was estimated by a one-point calibration using conditions existing in 1962 and assumed thereafter to be a constant.

The model output was the instantaneous lake phosphorus concentration at noon each day.

Simulated Lake Phosphorus Concentrations

Figure 2 shows the rapid drop in $P_i(t)$ following sewage diversion, the lake response $P_L(t)$ as calculated from the annual mean inflow concentration from 1962 to 1978 and the measured values of lake phosphorus. The predicted lake phosphorus matches the measured values very well considering that the input data were interpolated from annual averages and both the measured and the predicted lake concentration were instantaneous values. Note, in particular, that the model P_L represents the measured P_L well both before and after diversion, in addition to predicting the exponential recovery phase. The match between predicted and measured lake phosphorus before the

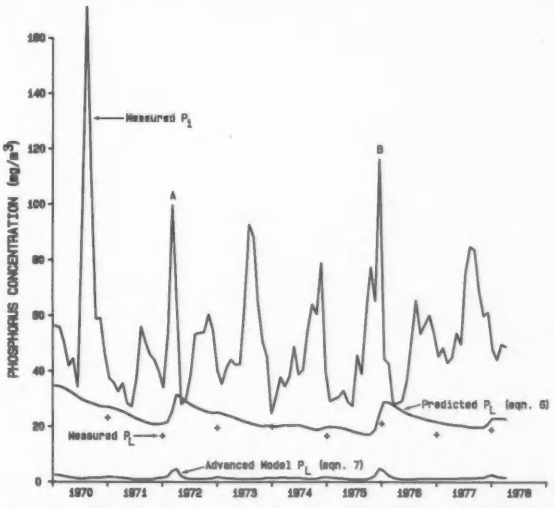

FIG. 3. Simulated responses of P_L, the concentration of total phosphorus in Lake Washington, produced by P_i, the monthly mean values of the phosphorus inflow measured from 1970 to 1978. The instantaneous lake concentration of total phosphorus measured on January 1 of each year are also shown.

diversion is simply a reflection of the one-point model calibration for 1962. To accurately simulate both the exponential decay and the final asymptote, however, requires both time scales to be correct. This dynamic constraint represents a stringent test of the model (see equations (3) and (5) and the earlier discussion of Fig. 1).

Figure 3 shows additional model results using the measured monthly mean data from 1970 to 1978. The monthly forcing P_i in Fig. 3 is substantially more variable than the annual forcing shown in Fig. 2. In spite of increased fluctuations in the inflow phosphorus, the instantaneous lake phosphorus concentrations predicted by the model are similar in both figures. In fact, P_L in Fig. 3 matches the measured values better than the P_L in Fig. 2. Because the model can only simulate a response to the data input, the more closely the input represents the actual forcing of the lake the better is the expected result. Presumably, weekly (or even daily) input data would produce an even better simulation.

Steady-State Models

For comparison, P_L was also simulated using the results of a steady-state phosphorus loading model (Vollenweider 1968, 1975, 1976). The concept of phosphorus loading to a lake, $L = P_i\, Q/A$, was used by Vollenweider when evaluating lake response to elevated inputs of phosphorus from municipal and industrial sources. Because the concentration of phosphorus in a lake clearly scales with the inflow concentration and not with the loading to the lake (see equation (3)), the phosphorus loading concept is of little value in a dynamic framework. Instead, the results of Vollenweider's steady-state models are applied here using the fundamental variables given in equation (1).

The conservation of mass equation is the basic starting point for both steady-state and dynamic models. For example, equation (2) is mathematically equivalent to the nonconservative phosphorus loading model presented by Vollenweider (1975, p. 58). To distinguish it from Vollenweider's earlier models, we will refer to it as the advanced model.

The advanced model evolved from equation (2) by incorporating the results of a regression analysis between P_L/P_i and τ_w using spring phosphorus data from 21 lakes and annual mean values of τ_w (Vollenweider 1976). The data were scattered about a regression line that was strongly influenced by two lakes with large values of τ_w. Vollenweider did not use the actual regression equation in his steady-state model but rather an analytical expression that better represented the asymptotic behaviour of P_L/P_i near $\tau_w = 0$. A relationship between the two time scales (i.e. $\tau_s = \sqrt{\tau_w}$) follows directly from this analytical equation.

Vollenweider only applied this relationship in his steady-state advanced model. It is possible, however to use Vollenweider's result for a dynamic simulation of P_L by substituting the relationship into the differential equation governing phosphorus for the advanced model. Then equation (2) becomes,

$$(7)\qquad \frac{dP_L}{dt} = \underbrace{\frac{P_i Q}{Az}}_{\text{(source)}} - \underbrace{\frac{P_L}{\tau_w}}_{\text{(sink)}} - \underbrace{\frac{P_L}{\sqrt{\tau_w}}}_{\text{(sink)}} .$$

Note that, although equation (7) contains one source term and two sink terms, the two sink terms are not independent. The sedimentation sink is now a function of water renewal. Rather than a model based on two independent time scales (τ_w, τ_s), the advanced model depends solely on the water renewal time, τ_w.

A strong advantage of equation (7) is that no calibration is required to simulate to the dynamics of total phosphorus in any lake. If it works for one lake, it should work for all lakes. Furthermore, only two inputs, $P_i(t)$ and $\tau_w(t)$, are needed to predict P_L and both inputs can be readily measured.

Equation (7) was applied to the Lake Washington data without explicit consideration of the confidence limits associated with Vollenweider's regression analysis. Unfortunately, P_L obtained from equation (7) does not simulate the measured lake concentrations very well (Figs. 2 and 3). The values of P_L calculated from Vollenweider's advanced model are an order of magnitude less than the P_L measured in Lake Washington. These small values of concentration indicate that the sedimentation sink is far too dominant in Equation (7).

The reason for the failure of the advanced model when applied to a dynamic simulation of Lake Washington is rooted in Vollenweider's regression analysis. All of the phosphorus loading models described in Vollenweider (1975, 1976) make use of the assumption that the 21 lakes were in a steady state with respect to phosphorus. If this assumption were true equation (7) should accurately model the dynamics of total phosphorus, at least, in these 21 lakes. Unfortunately, the potential margin for error when ignoring the time dependent term in the differential equation is very great. When the steady state assumption is made incorrectly (i.e. by assuming lakes are in equilibrium when they are not), the error is simply rolled up and included in the calculation of the sedimentation term. The most likely result is an over-estimation of the effects of sedimentation. While it is outside the scope of the present paper, a detailed assessment of the impact of the steady state assumption on Vollenweider's advanced model may be found in Kenney (1990)

Effect of Flooding on Total Phosphorus in Lake Washington

Comparing the fluctuations in P_i with the lake response in Figs. 2 and 3 clearly shows a fundamental characteristic of the

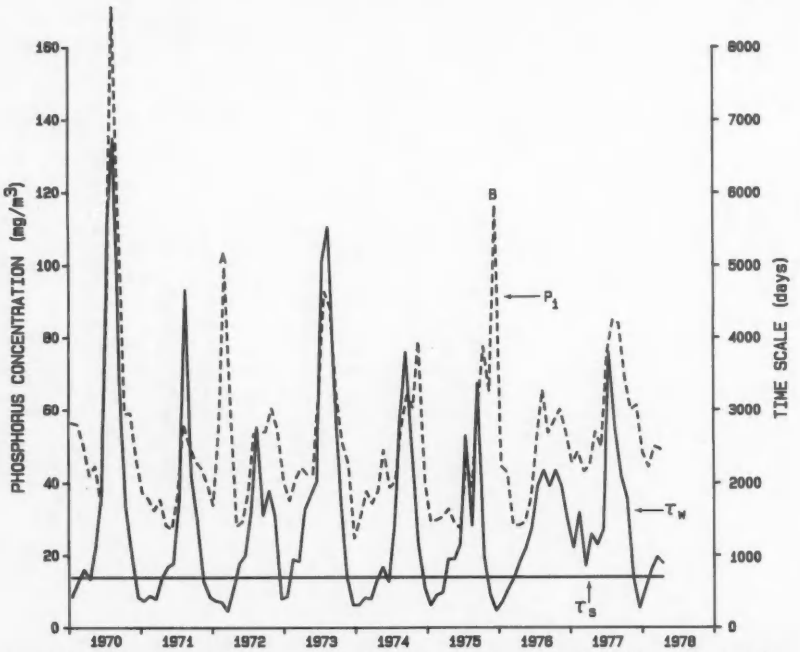

FIG. 4. Time scales input to phosphorus dynamics model (equation (6)) for the 1970 to 1978 simulation. The water renewal time scale, τ_w, was calculated from the measured monthly discharge. The sedimentation time scale, τ_s, was assumed constant. The forcing $P_i(t)$ for the model was the monthly mean concentration of total phosphorus input to Lake Washington. Daily values required for input to the model were linearly interpolated from the monthly data.

dynamics of total phosphorus in lakes. Forcing frequencies that are too high for the lake to respond are eliminated from the output while low frequencies are closely followed by the lake with little or no attenuation.

In both Figs. 2 and 3, the simulated P_L also has two significant peaks, one in the spring of 1972 and a second in the fall of 1975. These P_L peaks appear to be a response to the peaks in inflow phosphorus marked A and B. The question arises, therefore, why does the lake respond to the inflow peaks denoted A and B but not to other more intense peaks?

The answer may be found in Fig. 4, which shows the time scales which define the phosphorus dynamics of the model, τ_w and $\tau_s = 1/\sigma$, in addition to P_i. Note in Fig. 4 that most peaks in inflow phosphorus occurred during periods of low discharge (i.e. high values of τ_w). An inverse relationship between discharge and inflow concentration is typical of many lakes because large runoff tends to dilute chemical constituents in the inflow, particularly if the runoff is melt water. These P_i peaks were entirely damped and had no effect on the lake phosphorus because the overall time scale of the lake at the time of each peak was too long to permit the lake to respond. The two P_i peaks marked A and B did produce corresponding peaks in P_L, however, because the lake was dynamically able to respond at the time they occurred (i.e. τ_w (and τ_o) was small when P_i was large).

The A and B peaks resulted from the only two floods that occurred in Lake Washington's watershed from 1962 to 1978. During floods, high values of P_i coincide with high discharge because rivers overflow their banks and increase erosion of total phosphorus from soils not normally submersed. Edmondson and Lehman (1981) noted that the increase in P_i during the two floods was due to an increase in particulate phosphorus (P) with the dissolved P remaining relatively constant. Although the two floods produced significant lake response in the simulated P_L using both annual and monthly mean input data, the once a year temporal resolution of the P_L measured by Edmondson and Lehman is not high enough to verify the occurrence of these peaks in the lake.

Discussion

My model results suggest that two independent time scales, water renewal and sedimentation, are sufficient to represent the phosphorus dynamics of Lake Washington. Moreover, the success of a constant value for the sedimentation time scale suggests that there is no long term trend in the rate of phosphorus sedimentation. This was expected because both physical and biological processes controlling sedimentation are likely to be stationary over the long term. Because Lake Washington does not freeze over in winter, the physical processes that control sedimentation may also be relatively constant throughout the year. Measurements of sedimentation flux presented in Edmondson and Lehman (1981), however, suggest that sedimentation may be correlated with algal bloom events on a time scale less than 1 yr. Unfortunately, sufficient data are not available to resolve the question of short-term time dependence of the sedimentation time scale. Certainly, a constant value of τ_s allows a reasonably accurate simulation of both the exponential recovery phase and the asymptotic concentration of total phosphorus in Lake Washington. On the other hand, a dynamic sim-

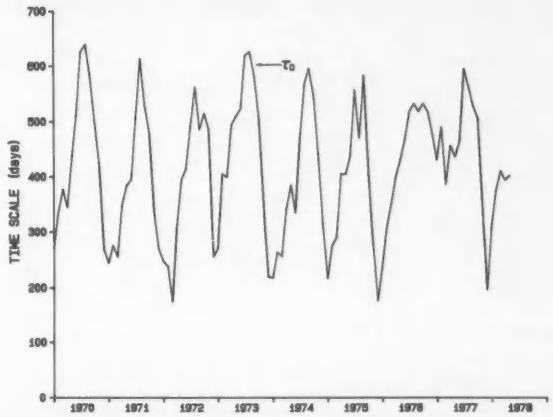

FIG. 5. Overall time scale, τ_o, controlling the dynamics of total phosphorus in Lake Washington.

ulation based on Vollenweider's advanced model with $\tau_s = \sqrt{\tau_w}$ underestimated the concentration of total phosphorus in Lake Washington by an order of magnitude.

It is premature to extrapolate these results too far because the Lake Washington data are unique, not only in the step function change in inflow phosphorus but also in the quality of the data and the length of the record. The rather small value of the sedimentation time scale (706 d) obtained for Lake Washington, however, is noteworthy. If other large lakes with physical characteristics similar to Lake Washington have similar sedimentation time scales then sedimentation would dominate the overall lake response regardless of very long water renewal times. The overall time scale of total phosphorus, τ_o, clearly shows the influence of sedimentation in Lake Washington (Fig. 5). During the summer months when the water renewal time scale becomes very large, the overall time scale approaches an upper limit equal to the sedimentation time scale. This means, for example, that a lake with a very long water renewal time, like Lake Superior or Lake Tahoe, might respond to phosphorus removal schemes at about the same rate as Lake Washington. While some physical arguments can be advanced in support of similarity in sedimentation in very large lakes, hard evidence is lacking. On the other hand, lakes shallow enough to be subject to sediment resuspension are expected to be very different. Shallow lakes are likely to require a time dependent τ_s for successful modelling.

In conclusion, total phosphorus concentrations in Lake Washington were successfully modelled over a 16-yr period using first-order linear dynamics. Two independent time scales, based on water renewal and sedimentation, are adequate to define the lake phosphorus dynamics. The water renewal time scale was highly variable throughout the year. On the other hand, the sedimentation time scale was successfully modelled as a constant with a value of 706 d. Further work is required to determine if sedimentation behaves similarly in other lakes.

Two floods that occurred during the 16-yr period had a marked effect on the simulated total phosphorus in the lake. These flood periods were the only occasions when high concentrations of total phosphorus in the inflow coincided with high flows. All other peaks in inflow phosphorus had little effect on the lake concentration because they occurred at times when the lake was dynamically unable to respond.

Acknowledgements

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A Comparison of the Growth of Vertically-Migrating and Nonmigrating Kokanee (*Oncorhynchus nerka*) Fry

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Johnston, N. T. 1990. A comparison of the growth of vertically-migrating and nonmigrating kokanee (*Oncorhynchus nerka*) fry. Can. J. Fish. Aquat. Sci. 47: 486–491.

A comparison of the growth of vertically-migrating kokanee (*Oncorhynchus nerka*) fry and nonmigrating fry confined to the epilimnion in thermally-stratified Kootenay Lake, British Columbia rejected the bioenergetic efficiency hypothesis for the adaptive significance of vertical migration. Growth rates were higher for nonmigrating fry than for vertically-migrating fry. Geometric mean wet weights in early October were 2.88 g for nonmigrating fry and 1.40 g for vertically-migrating fry of the same stock. The geometric mean weight of fry of a second stock rearing in the isothermal West Arm, in which behavioural thermoregulation by vertical migration was not possible, was 8.54 g in early October.

Une comparaison de la croissance des alevins de saumon kokani (*Oncorhynchus nerka*) migrant verticalement et des mêmes alevins non migrants confinés dans l'épilimnion du lac thermiquement stratifié Kootenay en Colombie-Britannique est venue infirmer l'hypothèse de l'efficacité bioénergétique émise pour expliquer l'importance de la migration verticale pour l'adaptation. Les taux de croissance étaient supérieurs chez les alevins non migrants que chez les alevins migrants. Les poids humides en moyenne géométrique au début d'octobre étaient de 2.88 g pour les alevins non migrants et de 1.40 g pour les alevins migrant verticalement appartenant au même stock. Le poids moyen géométrique des alevins d'un deuxième stock se reproduisant dans la bras ouest isotherme, dans lequel la thermorégulation du comportement par migration verticale était impossible, était de 8.54 g au début d'octobre.

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Underyearling *Oncorhynchus nerka* rearing in the limnetic areas of thermally-stratified lakes typically show a pattern of diel vertical migration in which fry pass the daylight hours in cold, food-poor hypolimnial waters and ascend at dusk to feed briefly in warmer, food-rich epilimnial waters (Narver 1970; Levy 1987). Light and temperature appear to be proximate factors regulating this migratory behavior (Narver 1970; Levy 1989). Levy (1987) reviews several single-factor hypotheses that have been proposed as the ultimate cause of the diel vertical migration of sockeye (anadromous *O. nerka*) and kokanee (nonanadromous *O. nerka*) fry. These include energetic efficiency, predator avoidance, and foraging strategy.

The hypothesis of behavioral thermoregulation to maximize growth under food-limited conditions (Brett 1971, 1983) is supported by rearing experiments that simulated the temperature regimes encountered by migrating fry (Biette and Geen 1980), however, these experiments did not include the energetic costs of vertical migration, which may be considerable (Levy 1987). Levy (1987) suggested that by remaining in the epilimnion during the day the visually-feeding fry could obtain higher growth rates as a consequence of increased foraging opportunities. A simple direct test of the bioenergetic hypothesis would be to compare the growth of vertically-migrating fry and nonmigrating fry confined to the epilimnion: vertically-migrating fry are expected to attain larger size if the bioenergetic hypothesis is correct.

Kokanee fry in Kootenay Lake, British Columbia vertically migrate (Levy 1989) whereas their zooplankton prey do not (Zyblut 1967). The mean weights of underyearling kokanee in the main body of the lake ranged from 1.2 to 2.0 g (wet weight) in mid-October, 1984–87 (Parkinson 1988), which strongly suggests that fry growth was food-limited as *O. nerka* fry in some food-rich, thermally-stratified lakes can attain weights of 11–12 g by October (e.g. Eggers 1978). The lake is thermally-stratified throughout the summer growing season (Zyblut 1970). Thus the conditions under which the bioenergetic hypothesis predicts higher growth in a vertically-migrating population are met.

I tested the bioenergetic hypothesis by comparing the growth of kokanee fry that were experimentally confined in the epilimnion against that of vertically-migrating fry of the same stock. I tested the hypothesis that the size of the vertically-migrating fry was greater than the size of the nonmigrating fry using a one-tailed *t*-test, with the null hypothesis that the size of vertically-migrating fry was the same as or less than that of the nonmigrating fry.

Methods

The growth of nonmigrating and vertically-migrating kokanee fry were compared at monthly intervals from May to October, 1988 by monitoring the sizes of pen-reared (nonmigrating) and trawl-caught (vertically-migrating) wild fry of the same

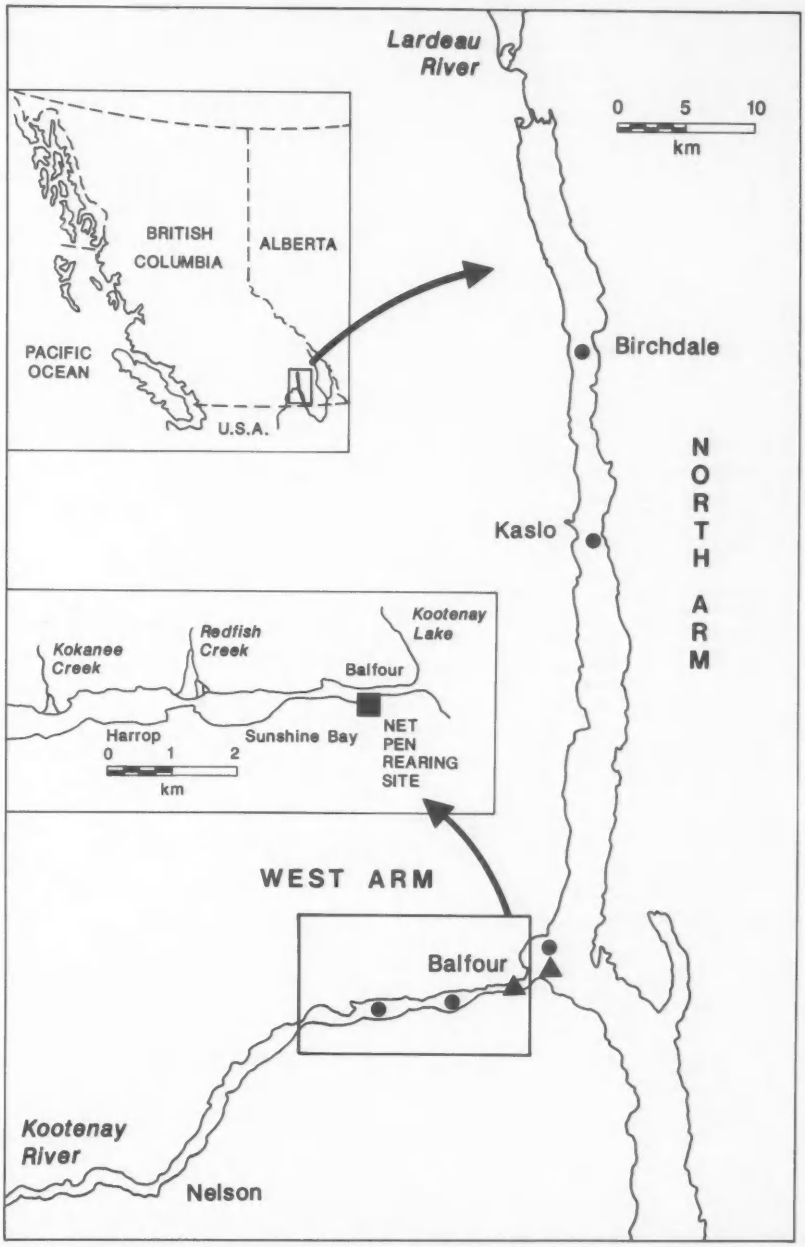

FIG. 1. North and West Arms of Kootenay Lake, showing sampling sites. ● indicates trawl sampling sites, ▲ zooplankton and temperature sampling sites, and ■ the net pen site.

stock. Kokanee fry were collected from the Meadow Creek spawning channel on 19 May during the peak of the fry emigration and were transported to net pens at Balfour, on the West Arm of Kootenay Lake (Fig. 1). The Meadow Creek-Lardeau River stock is the most abundant kokanee stock in Kootenay Lake and accounts for 80% of the adult escapement in the lake (Andrusak 1981). Fry were reared from 19 May to 8 October in four replicate, covered, 1.2×1.2 m (width) $\times$ 3m (depth) pens constructed of 6 mm (stretched-mesh), 210-10 nylon netting. The pens were anchored 50 m apart in 8 to 10 m of water. Initial densities were 55 fish per pen (12.7 fish$\cdot$m^{-3}). Losses of fry from the pens, however, reduced densities to 3.9 to 10.9 fish$\cdot$m^{-3} within the first month (Table 1). Fry densities in the pens were considerably greater than those in the main lake, which averaged about 400 fry$\cdot$ha^{-1} in October (Parkinson 1988). The West Arm is the outflow from the main lake, so that

TABLE 1. Survivorship of kokanee fry in four replicate net-pens in the epilimnion of Kootenay Lake, 1988. Number of fry alive at sampling dates. Initial losses were from fry escaping rather than mortality.

Date	Pen 1	Pen 2	Pen 3	Pen 4
19 May	55	55	55	55
14 June	17	30	47	44
14 July	15	24	42	43
12 August	15	23	42	42
7 September	15	22	42	41
8 October	14	1	39	0

there was a slight current (maximum about 0.1 $m \cdot s^{-1}$) at the net-pen site, but there was no detectable current (<0.01 $m \cdot s^{-1}$) inside the net-pens. The net-pens were cleaned every second day.

At monthly intervals, the fry were removed and transported in insulated containers to a nearby laboratory where a random sample of 25 fish from each pen (or all fry if fewer than 25) was anaesthetized in 2-phenoxyethanol solution, damp-dried on paper towelling, weighed to the nearest milligram on an electronic balance and returned to the same pen. Weight data were log-transformed prior to statistical comparisons to improve normality and homogeneity of variances; weights are reported as geometric means after back-transformation to the original units.

Zooplankton densities were sampled at mid-day inside the net-pens and in the uppermost 25 m of the water column at the rearing site and the main lake by making replicate vertical hauls with a 25-cm, 153-μm mesh Wisconsin net. Vertical temperature profiles were measured with a YSI model 57 temperature-oxygen meter.

Vertically-migrating fry were captured with a mid-water trawl at night when the fry were in the near-surface waters. Fry position in the water column was monitored with a Furuno model 22 echo-sounder using 40 log$R$ time-varied gain at 200 kHz. The trawl had a mouth opening of 5×5 m and was towed for 45 min at about 1 $m \cdot s^{-1}$ at depths between 10 and 25 m. Vertically-migrating fry were collected at several locations in the North Arm as the Meadow Creek stock dispersed down the lake during the summer. Fish were preserved on ice and weighed the following day.

Fry were also collected in Sunshine Bay and Harrop Basin on the West Arm (Fig. 1). These fry are a separate stock (Vernon 1957) which emerged 2–3 wk earlier than the North Arm stock and reared in an isothermal environment (see below) in which behavioral thermoregulation by vertical migration was not possible.

Results

The main lake was thermally stratified throughout the study period, the thermocline occurring between 20 and 30 m (Fig. 2). The shallower West Arm was isothermal (Fig. 2). Mean temperatures in the upper 25 m of the main lake and the West Arm were the same within 0.3°C, except in July when the difference was 2.1°C. Thus, fry reared in the net-pens experienced temperatures very similar to those of the epilimnion of the main lake.

The zooplankton community at the rearing site was an outwash community from the epilimnion of the main lake. The species composition of the zooplankton was similar at all sites (Table 2). Moreover, average densities of zooplankton in the upper 25 m were very similar in the West Arm and the main

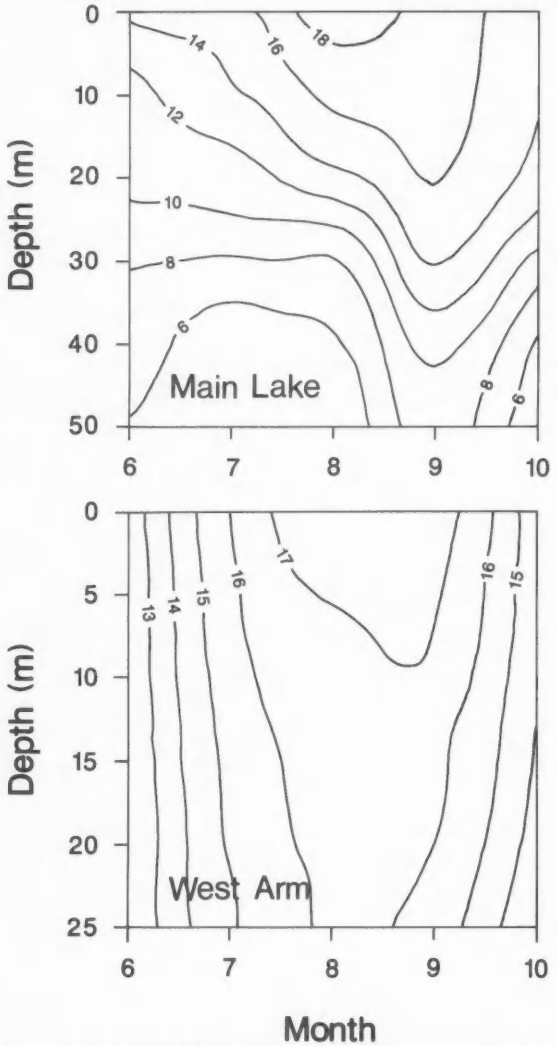

FIG. 2. Temperature isopleths for the main lake (upper panel) and the West Arm (lower panel) during 1988.

lake (Fig. 3). Mean zooplankton densities did not differ between the main lake and the West Arm at any sampling date (t-tests, $p = 0.17$ to 0.53). Mean zooplankton densities within the net-pens, however, were much lower (Fig. 3), presumably as the result of filtering by the net and foraging by the penned fry. Thus, the standing stock of food for the pen-reared fry was less than or equal to that found in the epilimnion of the main lake.

Fry in the main lake migrated between the hypolimnion and the epilimnion. Kokanee fry in the main lake were observed on echograms between 10 and 30 m after dusk and were caught in trawls fishing this depth range. Levy (1989) presented data showing the daytime depth distribution of fry to be between 30 and 100 m, with two-thirds of the population below 50 m.

The geometric mean weights of vertically-migrating and nonmigrating North Arm fry were identical (t-test, $p > 0.1$) in mid-June (Fig. 4). Thereafter, the mean weights of the fry con-

TABLE 2. Percent composition of the zooplankton in the main lake, the West Arm and inside the net pens, summer 1988.

	June	July	August	September	October
Main Lake ($n=2$)					
Bosmina sp.		1.5	18.2	6.1	6.0
Diaphanosoma sp.		0.4	6.3	9.3	10.6
Diaptomus ashlandi	33.4	46.1	16.6	7.6	11.6
Cyclops bicuspidatus	65.8	52.0	59.0	78.3	71.0
West Arm ($n=2$)					
Bosmina sp.		0.9	28.3		4.1
Diaphanosoma sp.	0.5	1.3	11.7		15.0
Diaptomus ashlandi	35.9	48.7	9.1		7.6
Cyclops bicuspidatus	62.5	48.1	56.5		69.7
Net Pens ($n=4$)					
Bosmina sp.		0.6	24.4	2.4	
Diaphanosoma sp.		0.1	27.5	13.1	
Diaptomus ashlandi	52.8	33.7	9.8	18.0	
Cyclops bicuspidatus	47.2	66.1	37.6	64.9	

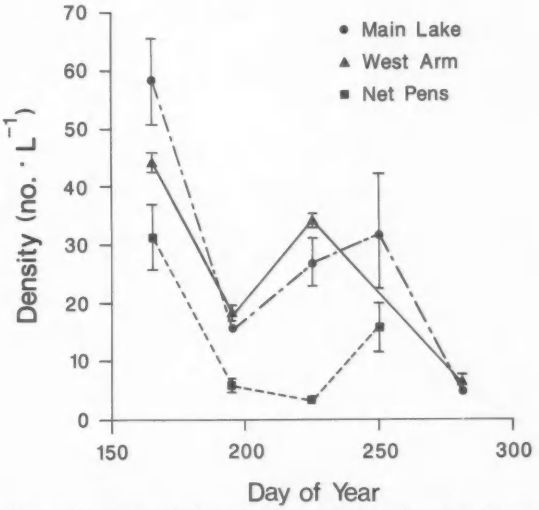

FIG. 3. Average zooplankton densities (± SE) in the upper 25 m of the main lake and the West Arm and inside the net pens during summer 1988.

fined to the epilimnion were greater than those of vertically-migrating fry (t-tests, $p<0.001$, Fig. 4). By early October, the geometric mean weight of the pen-reared fry (2.88 g) was twice that of the vertically-migrating wild fry (1.40 g). Average instantaneous growth rates over the period from fry emergence to early October were 2.66%·d^{-1} for the pen-reared fry and 2.14%·d^{-1} for the trawl-caught fry. The instantaneous growth rates of the penned fry varied inversely with fry size and density but the dependence on fry density was slight over the range in the four pens (Fig. 5).

The geometric mean weights of underyearling kokanee caught in the isothermal West Arm were considerably greater than those of trawl-caught North Arm fry on corresponding dates (Fig. 4). By early October, West Arm fry averaged 8.54 g. Their average instantaneous growth rate from early May to October was 2.86%·d^{-1}.

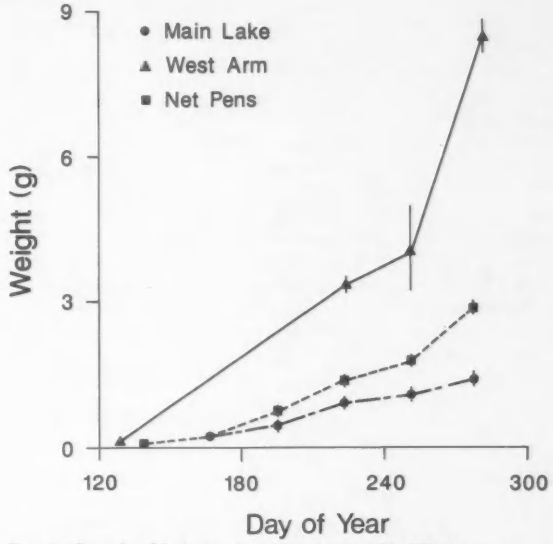

FIG. 4. Growth of kokanee fry throughout 1988. Weights are geometric means, vertical bars are 95% CL. Fry that migrated vertically between the epilimnion and the hypolimnion (main lake fry) grew more slowly than fry that reared in the epilimnion (net pen and West Arm fry). West Arm fry weights in May are for emigrants from the Kokanee Creek spawning channel.

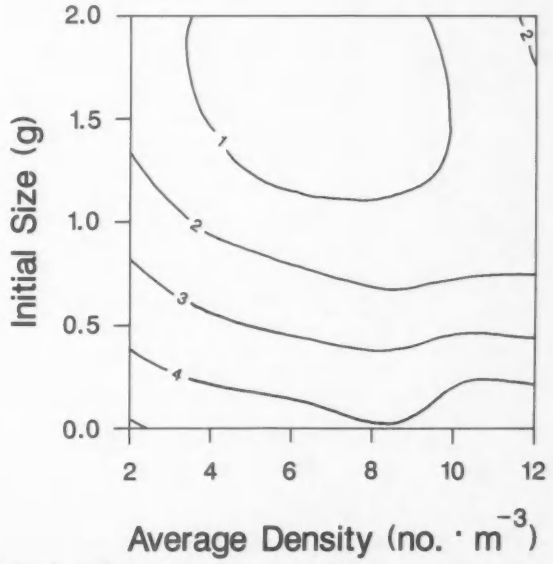

FIG. 5. Isopleths of instantaneous growth rates (percent per day) as functions of fish size and density for fry in the net pens.

Discussion

The observation that kokanee fry reared in epilimnial waters grew to larger size than vertically-migrating fry is inconsistent with the bioenergetic efficiency hypothesis. The result suggests that either other single-factor hypotheses, such as predator avoidance (Eggers 1978), may apply or that multi-factor

hypotheses such as a trade-off between predation risk and energy returns (Clark and Levy 1988) must be invoked to account for the behavior. Levy (1987) advanced two other arguments against the bioenergetic hypothesis as the sole explanation for vertical migration in underyearling *O. nerka*. First, the hypothesis is not consistent with observations of vertical migration under isothermal conditions. Second, a reversed migration pattern would expose fry to similar temperature regimes but increased feeding opportunities, and thus should be favoured.

Although the experimentally nonmigrating kokanee fry were reared in the West Arm rather than in the epilimnion of the main lake, their growth should represent the minimum growth of nonmigrating fry in the main lake as conditions of temperature, food abundance, and fish density were identical to or less favourable than conditions in the epilimnion of the main lake. Because of the slight (about 0.1 $m \cdot s^{-1}$) current at the pen site, prey availability in the pens may have been increased by the rate of delivery of zooplankton by the current. However, zooplankton abundances within the pens were reduced compared with the external environment and current was undetectable within the pens. Moreover, fry foraging in the epilimnion of the main lake could obtain the same encounter rate and potential food availability by increasing their swimming speed. Similarly, the slight difference in mean epilimnial temperature seen in July between the West Arm and the main lake could be eliminated by behavioral thermoregulation within the epilimnion. The much greater weight attained by free-ranging fry in the West Arm suggests that conditions within the pens reduced, rather than increased, the growth differences between the nonmigrating and vertically-migrating North Arm fry, although earlier emergence was partly responsible for the larger size of the West Arm fry.

Because size and mortality are closely linked in the early life of *O. nerka*, strong selection for behavior that permits increased growth would be expected. Survival of *O. nerka* through the first summer of life is about 25–35% (Foerster 1938; McDonald and Hume 1984). Mortality on sockeye salmon fry is size-selective; in Babine Lake fry smaller than the median size suffered mortality rates seven times greater than the larger fry (West and Larkin 1987). The sources of mortality in fry are not well-established, but it is likely that predation accounts for much of the loss, as Foerster and Ricker (1941) demonstrated increased survival of young sockeye salmon after predator reductions within a nursery lake. Other studies have shown predation to be a significant mortality agent in some populations of young salmon (Ricker 1941; Parker 1968). Many other studies have also suggested that smaller salmonids are more vulnerable to predators than are larger ones (Bams 1967; Parker 1971; Hargreaves and LeBrasseur 1986). The increased susceptibility of smaller salmon to predation may have a mechanical basis, through burst-swimming speeds that vary with body size (Taylor and McPhail 1985). Smaller *O. nerka* fry are also more susceptible to infection by the parasite *Eubothrium salvelini* (Boyce 1974), whose presence may reduce fry viability as well as increasing susceptibility to predation by reducing swimming performance (Boyce 1979). Thus, small size differences may have important consequences to fry survival.

As vertical migration did not maximize growth in the Kootenay Lake kokanee population despite the advantages of increased size (above), other selective factors must be operating to shape the migratory behavior. A model that balanced increased energetic returns against predation risk (Clark and Levy 1988) predicted the qualitative features of the vertical migrations observed in *O. nerka* fry, which suggests that a multifactor hypothesis is more probable.

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Plant Pigments as Tracers of Emergent and Submergent Macrophytes from the Hudson River[1]

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Bianchi, T. S., and S. Findlay. 1990. Plant pigments as tracers of emergent and submergent macrophytes from the Hudson River. Can. J. Fish. Aquat. Sci. 47: 492–494.

Ratios of photosynthetic pigment concentrations in aquatic macrophytes can provide a useful way to differentiate between inputs of emergent versus submergent macrophytes into aquatic food webs. Using reversed-phase HPLC we examined the distribution of carotenoid and chlorophyll pigment markers in eight macrophytes from the tidal freshwater portion of the Hudson River. Lutein was the most abundant carotenoid in all macrophytes, and concentrations in the emergent forms were significantly higher. Chlorophyll-*b* showed significantly higher concentrations in the submerged macrophytes than in the emergent forms. The chlorophyll-*b*/lutein ratio may be a useful marker to distinguish between organic inputs of submergent and emergent forms of macrophytes in aquatic ecosystems.

Les ratios de concentrations de pigments photosynthétiques dans les macrophytes aquatiques peuvent se révéler un outil utile pour établir la différence entre les apports de macrophytes émergés et de macrophytes partiellement submergés dans la chaîne alimentaire aquatique. À l'aide de la chromatographie liquide à haute performance en phase inverse, nous avons examiné la distribution de marqueurs pigmentaires caroténoïde et chlorophylle présents dans huit macrophytes de la portion tidale d'eau douce de l'Hudson. La lutéine était le caroténoïde le plus abondant dans tous les macrophytes et ses concentrations dans les formes émergées étaient considérablement plus élevées. La chlorophylle-*b* affichait des concentrations de beaucoup supérieures dans les macrophytes partiellement submergés que dans les formes émergées. Le ratio chlorophylle-*b*/lutéine pourrait être un marqueur utile pour faire la distinction entre les apports organiques de forme submergée et immergée de macrophytes dans les systèmes aquatiques.

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Macrophytes have been shown to be important resources in the food webs of lakes, wetlands, and riverine ecosystems (Brinson et al. 1981; Moeller 1985). Because of the diverse assemblage of macrophytes usually found in these systems, it is generally difficult to identify the relative importance of these materials in food webs. Characteristic pigments from different classes of plants can be used as bio-markers to trace organic matter flow in natural systems (Gorham 1960; Daley 1973; Watts et al. 1977; Repeta and Gagosian 1987; Carpenter et al. 1988). Chlorophyll and carotenoid pigments, which are found in all plants, exhibit class-specificity (Mantoura and Llewellyn 1983), and are therefore good markers for distinguishing between different inputs of plant material to aquatic systems. Several good markers have already been identified for different types of phytoplankton. For example, the carotenoid fucoxanthin is a marker for diatoms (Wright and Jeffrey 1987) while zeaxanthin can serve as a marker for blue-green algae (Gieskes and Kraay 1983). Macrophytes contain chlorophyll-*b* which is not found in diatoms or blue-greens (Jeffrey 1974). However, it is difficult to distinguish between the relative importance of emergent versus submergent macrophytes to aquatic food webs. In small lakes, input of organic matter from fringing emergent macrophytes or submerged macrophytes may be a significant fraction of total primary production (table 15-15 in Wetzel (1975)). Also, detritus inputs from riverine macrophytes may be important in riverine ecosystems (e.g. Wallace and O'Hop 1985). In this note we report plant pigment ratios that may help in distinguishing between emergent and submergent macrophytic sources.

Materials and Methods

Eight macrophyte species were collected from the mid-Hudson River near Kingston, NY the Tivoli Bays (Table 1). All macrophytes considered in this study were rooted vascular plants. This portion of the river has a tidal range of about 1 m and is broad and shallow. The salt front (0.1 g Cl/L) only reaches this area during periods of extreme drought. Beds of submerged macrophytes are common in areas less than 2 m deep, and two of the larger tidal freshwater wetlands (the Tivoli Bays) are located in this area. The macrophytes chosen for this study represent several of the dominant forms of macrophytes in this portion of the Hudson River.

Five grams (wet weight) of each of the macrophytes were lyophilized, reweighed, and then extracted using 100% acetone. Pigment extracts were ground, sonicated for 5 min, and allowed to stand overnight in the dark at 4°C prior to centrifugation. From a series of repeated extractions we estimated an extraction efficiency of 90% using our procedure. Pigments

[1]Contribution to the program of the Institute of Ecosystem Studies, New York Botanical Garden.

TABLE 1. Carotenoid and chlorophyll concentrations (μg/g dry wt.) in eight macrophytes collected from the Hudson River. Numbers in parentheses represent standard deviation (sample size $N = 2$).

Plants	Chl-*a*	Chl-*b*	Violaxanthin	Neoxanthin	Lutein	β-carotene
(Emergent forms)						
Typha angustifolia	235.18	99.83	52.04	26.09	75.62	22.38
	(24.46)	(18.36)	(12.45)	(5.19)	(24.12)	(5.78)
Nuphar advena	567.29	189.00	38.01	24.13	156.19	32.15
	(51.23)	(21.48)	(6.78)	(5.68)	17.36)	(3.98)
Pontederia cordata	649.83	248.57	62.48	42.13	222.04	32.18
	(45.12)	(28.24)	(13.34)	(11.45)	(32.12)	(4.14)
Trapa natans	531.86	132.96	43.98	23.64	103.07	25.86
	(43.12)	(21.45)	(5.34)	(3.76)	(22.76)	(8.92)
Scirpus fluviatilis	321.59	126.33	24.68	28.43	120.93	32.86
	(24.26)	(19.34)	(2.46)	(7.12)	(15.94)	(6.12)
(Submergent forms)						
Vallisneria americana	376.84	198.82	12.61	20.83	54.17	6.89
	(38.16)	(18.93)	(2.17)	(1.27)	(6.34)	(1.01)
Potamogeton sp.	410.48	263.57	15.39	12.43	60.48	7.38
	(56.87)	(23.45)	(2.18)	(1.98)	(14.87)	(1.92)
Myriophyllum sp.	438.38	237.39	23.41	58.69	61.15	24.39
	(67.12)	(34.19)	(2.76)	(10.64)	(12.98)	(6.38)

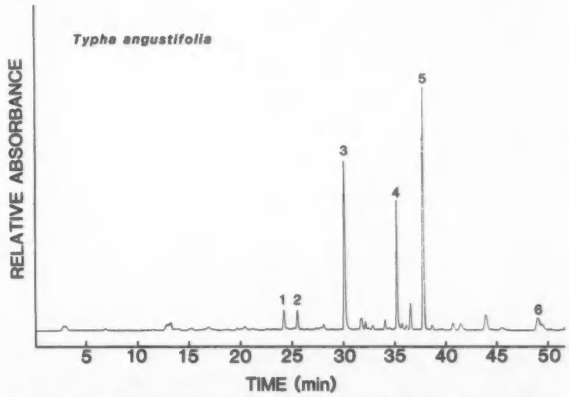

FIG. 1. Absorbance chromatogram of pigments in *Typha angustifolia*, analyzed by ion-pairing reversed-phase HPLC. Peaks are numbered as follows: 1, neoxanthin; 2, violaxanthin; 3, lutein; 4, chlorophyll-*b*; 5, chlorophyll-*a*; 6, β-carotene. The remaining larger peaks not identified are chlorophyll degradation products.

were determined by ion-pairing, reversed-phase HPLC (Mantoura and Llewellyn 1983).

The equipment employed consisted of a gradient pumping system (Varian-Vista 5500) controlled by a Vista 402 dual channel system. Dual channel detection was achieved with a Varian-Vista UV monitor set to 440 nm for absorbance and a Kratos Spectroflow 980 fluorescence detector, with excitation at 440 nm and emission at 700 nm. An auto-injector equipped with a Rheodyne model 7126 valve was connected via a precolumn to a reversed-phase C-18 Adsorbosphere column (5-μm particle size; 250 mm × 4.6 mm i.d.). After injection (100-μL sample), a gradient program that ramped from 100% mobile-phase A (80:10:10, methanol; water; tetrabutyl ammonium acetate) to 100% mobile-phase B (70:30, methanol; acetone) in 30 min with a hold for 20 min provided sufficient resolution of all pigments of interest (Fig. 1).

TABLE 2. Chlorophyll-*a*/*b* and chlorophyll-*b*/lutein ratios in eight macrophytes collected from the Hudson River.

Plants	Chl-*a*/*b*	Chl-*b*/lutein
(Emergent forms)		
Typha angustifolia	2.85	1.32
Nuphar advena	3.00	1.21
Pontederia cordata	2.61	1.12
Trapa natans	4.00	1.29
Scirpus fluviatilis	2.58	1.04
(Submergent forms)		
Vallisneria americana	1.89	3.67
Potamogeton sp.	1.56	4.36
Myriophyllum sp.	1.84	3.89

For selected samples, pigment identification was confirmed using a Waters 990 photo diode-array detector along with published values of absorption maxima for chloropigments and carotenoids (Davies 1976; Mantoura and Llewellyn 1983; Wright and Jeffrey 1987). For example, the HPLC method used here did not allow for peak resolution between zeaxanthin and lutein, thus diode array confirmation was necessary. Calibration standards for chlorophylly-*a*,*b* were obtained from Sigma Chemical Company.

Results

In the eight macrophytes studied, five major carotenoids were identified in addition to chlorophylls-*a* and *b* (Table 1). A typical absorbance chromatogram of one of the macrophytes (*Typha angustifolia*) is shown in Fig. 1. Lutein was the most abundant carotenoid in all eight macrophytes studied (Table 1). Concentrations of β-carotene were significantly higher (one-way ANOVA, $p<0.05$) in the emergent macrophytes than in the submergent forms. A multiple range test showed that β-carotene concentrations in *Myriophyllum* sp. were indistinguishable from concentrations in emergent forms (Table 1). The

three submerged forms of aquatic macrophytes (*Potamogeton* sp., *Vallisneria americana*, *Myriophyllum* sp.) had significantly lower (one-way ANOVA, $p<0.05$) chlorophyll-*a*/*b* ratios than the five emergent macrophytes (Table 2). The chlorophyll-*b*/lutein ratios were significantly higher (one-way ANOVA, $p<0.001$) in the three submerged forms than in the five emergent macrophytes (Table 2).

Discussion

The lower chlorophyll-*a*,*b* ratios observed in the submerged forms of macrophytes were due to the significantly higher concentrations of chlorophyll-*b* in these plants. Chlorophyll-*b* is one of the most widespread accessory pigments used for light harvesting efficiency found in chlorophytes (Wood 1979). To compensate for the limited amount of light in the turbid waters (extinction coefficients = 2 to 10/m) of the Hudson River, submerged macrophytes have higher concentrations of chlorophyll-*b*. These higher chlorophyll-*b* ratios, found in submergent macrophytes of the Hudson River, are also higher than in the marine submergent macrophytes, *Zostera*, and *Ulva*, found in less turbid systems (Bianchi et al. 1988). β-carotene serves as a photoprotectant in plants (Paerl et al. 1983). This may explain the higher concentrations of β-carotene in the emergent macrophytes which are exposed to more direct sunlight.

The three most abundant carotenoids found in chlorophytes are neoxanthin, violaxanthin, and lutein (Liaaen-Jensen 1978, 1985). There are significantly greater concentrations of lutein in the emergent forms of macrophytes than in the submergent forms (Table 1). The lower chlorophyll-*b*/lutein ratios in the emergent macrophytes may provide a good bio-marker for identifying the principal sources of macrophytic input to riverine systems. Despite the heterogeneity of organic matter (detrital and living) usually found in the water column of estuarine and riverine systems, field samples from this area of the Hudson indicate that seasonal differences in dominant and persistent pigment concentrations of source materials (i.e. emergent and submergent) are detectable (T. S. Bianchi and S. Findlay, unpubl. data). It should be noted that in less-turbid environments chlorophyll-*b* concentrations in macrophytes may not be as elevated, thus making the chlorophyll-*b*/lutein ratio more sensitive to differences in lutein concentrations.

We have looked at the chlorophyll-*b*/lutein ratio in abscised leaves from red maple (*Acer rubrum*) and they are even lower (0.26) than in the emergent macrophytes. This suggests that the chlorophyll-*b*/lutein ratio decreases along a gradient moving from aquatic to terrestrial systems. If so, this ratio may also provide a useful marker that distinguishes between terrestrial and aquatic plant sources in land-margin ecosystems.

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Filtering rates of *Diaptomus minutus, Bosmina* spp., *Diaphanosoma* sp., *Holopedium gibberum* (Crustacea), and Zooplankton Community Grazing Rates in Some Acidic and Circumneutral Ontario Lakes

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Filtering rates of several zooplankters and grazing rates of the zooplankton community were investigated in seven Ontario lakes ranging in mean pH from 4.6 to 7.1. Filtering rates of *Diaptomus minutus, Diaphanosoma* sp., and *Holopedium gibberum* were negatively correlated with lake pH and alkalinity; rates for these species averaged 89, 171, and 514 $\mu L \cdot ind^{-1} \cdot h^{-1}$, respectively in the circumneutral lakes, and 200, 374, and 1853 $\mu L \cdot ind^{-1} \cdot h^{-1}$ in acidic lakes. The filtering rate of *Bosmina* spp. was not correlated with lake pH; its average rates were 35 and 44 $\mu L \cdot ind^{-1} \cdot h^{-1}$ in circumneutral and acidic lakes, respectively. Other environmental parameters examined (temperature, light intensity, plankton biomass, chlorophyll *a* concentration) did not appear to influence the filtering rate of most species tested. Zooplankton community grazing rates were not correlated with lake pH; rates averaged 1.1 $\% \cdot h^{-1}$ in circumneutral lakes, and 1.5 $\% \cdot h^{-1}$ in acidic lakes. This result does not support a previous hypothesis that the efficiency of energy transfer from primary to secondary trophic levels is reduced by acidification. There was no indication that grazing pressure on small versus large cells changed at low pH, based on comparisons of community grazing rates on the small alga *Chlorella* and the larger *Cosmarium*.

Nous avons étudié le taux de filtrage de plusieurs zooplanctontes et le taux de broutage de la communauté zooplanctonique dans sept lacs ontariens présentant un pH moyen de 4.6 à 7.1. Le taux de filtrage de *Diapterus minutus, Diaphanosoma* sp., et *Holopedium gibberum* présentait une corrélation négative avec le pH et l'alcalinité des lacs; il atteignait respectivement pour ces espèces, en moyenne, 89, 171, et 514 $\mu L \cdot ind^{-1} \cdot h^{-1}$ dans les lacs presque neutres, et 200, 374, et 1853 $\mu L \cdot ind^{-1} \cdot h^{-1}$ dans les lacs acides. Le taux de filtrage de *Bosmina* spp. n'était pas corrélé au pH du lac; il était en moyenne de 35 et 44 $\mu L \cdot ind^{-1} \cdot h^{-1}$, respectivement dans les lacs presque neutres et les lacs acides. Les autres paramètres environnementaux examinés (température, éclairement, biomasse planctonique, concentration de la chlorophylle *a*) ne semblaient pas influer sur le taux de filtrage de la plupart des espèces étudiées. Le taux de broutage de la communauté planctonique n'était pas corrélé au pH du lac; ce taux était en moyenne de 1.1 $\% \cdot h^{-1}$ dans les lacs presque neutres, et de 1.5 $\% \cdot h^{-1}$ dans les lacs acides. Ce résultat informe une hypothèse antérieure selon laquelle l'efficience du transfert d'énergie du niveau trophique primaire au niveau secondaire serait réduite par l'acidification. Rien n'indiquait un report de la pression de broutage des petites cellules vers les cellules plus grosses en présence d'un pH bas, selon les comparaisons des taux de broutage de la communauté sur la petite algue *Chlorella* et la grosse algue *Cosmarium*.

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Although changes in community structure associated with acidification have been observed for phytoplankton and zooplankton, as well as for many other aquatic organisms (Almer et al. 1974; Harvey et al. 1981), mechanisms controlling the changes in plankton communities are as yet poorly understood. Alterations in zooplankton–phytoplankton relationships have been suggested as one type of mechanism which might be related to the observed changes in plankton communities with lake acidification (Roff and Kwiatkowski 1977; Yan and Strus 1980).

Changes in food characteristics may be potentially important determinants of zooplankton grazing, affecting the zooplankton community at low pH. The composition of the algal community in acidic lakes is certainly different from nonacidic lakes (Kwiatowski and Roff 1976; Stokes and Yung 1986), and the fraction available to herbivores for food may be reduced. For example, *Peridinium*, a common dominant in the phytoplankton of acidic lakes, may be unsuitable as a food source for herbivores because of its large size and hard theca (Yan and Strus 1980). Blue-green algae, which are abundant in some acidic waters, may be unpalatable or of low nutritional value for herbivores (Arnold 1971). In response to these changes in the phytoplankton community, zooplankton may increase their filtering rate in order to maximize collection of food particles, and there may be shifts in zooplankton species composition to herbivores that can efficiently utilize the existing phytoplankton community. Zooplankton filtering might also be influenced by pH per se.

Conversely, changes in the zooplankton community induced by acidification may influence the phytoplankton community. Zooplankton commonly dominant in North American acidic waters are small taxa; large cladocerans such as *Daphnia* are rare while the small *Bosmina longirostris* dominates, and the large herbivorous calanoid *Diaptomus oregonensis* is replaced by the smaller *D. minutus* (Sprules 1975; Confer et al. 1983). Since crustacean filtering rate has been shown to increase exponentially with body size (Burns 1969; Haney 1985), these small-bodied herbivores may remove algae at a lower rate. The predominance of small-bodied zooplankton in acidic lakes at densities equal to or lower than those at neutral pH may cause a decrease in grazing pressure on the phytoplankton community. This would reduce the transfer of energy from primary to secondary trophic levels, as has been hypothesized by Yan and Strus (1980). As well, the small-sized herbivores in acidic lakes may be unable to filter large algae (Burns 1968a), possibly altering phytoplankton community composition.

To clarify some of these uncertainties, we addressed three aspects of zooplankton–phytoplankton interactions:

1) Are there differences in the filtering rates of zooplankton species among lakes? If so, are these differences associated with pH or pH-related factors including changes in the phytoplankton food source?
2) Are there differences in the grazing rate of zooplankton communities which may be related to pH or to factors associated with pH?
3) Is there evidence that changes in size – specific grazing rates may play a role in causing observed changes in phytoplankton communities at low pH?

Methods

Study Area

Zooplankton were studied in seven lakes that are located on the Canadian Precambrian Shield, 35–55 km southwest of Sudbury. Most of the lakes lie in the La Cloche Mountains, in the area where acidification of Ontario lakes was first documented by Beamish and Harvey (1972). The lakes investigated varied in mean pH from 7.1 to 4.6. They were ultra-oligotrophic to meso-oligotrophic. Coordinates for the lakes are given in Bleiwas (1983).

Studies were conducted in July 1980, July 1981, and August 1981, and each lake was sampled on one to three occasions.

Physical, Chemical, and Biological Characteristics

Several factors that may influence zooplankton grazing rate were determined at each sample site. Most measurements were taken at two depths: a "subsurface" sample at 1 m and a "deep" sample at 5.5–8.0 m. Water pH was measured at both depths using a Portomatic pH meter calibrated with two buffers, allowing the reading to stabilize. Total inflection point alkalinity was determined within 24 h on samples from 1 m depth at each site (Ontario Ministry of the Environment 1979). Light transmission as percent of surface intensity was estimated from Secchi depth measurements, assuming light penetration is logarithmic (Beeton 1958; Wetzel 1975). Temperature and conductivity were measured at both depths, and oxygen concentration at the deep sample site.

Phytoplankton samples were collected at both depths using a 2-L van Dorn bottle. Samples fixed in Lugol's iodine were later identified and enumerated by the Utermohl technique (Utermohl 1958). Total phytoplankton numbers were counted, and edible phytoplankton biomass calculated from biovolumes determined using geometric approximations of measured cell dimensions for each species and assuming a specific gravity of 1.0 (Vollenweider 1969). Algae were assumed to be edible if their maximum dimension did not exceed 30 μm. Detrital particles were also counted, divided into categories <15, 15–30, and >30 μm in length, and detrital mass calculated. Samples were taken for chlorophyll *a* determination, using extraction with acetone, measured spectrophotometrically and corrected for phaeophytin (ASTM 1979).

Integrated zooplankton samples (0.5 m above bottom to surface) were collected on each occasion with a 150-μm mesh Wisconsin net, and preserved with 4–5% sugar-formalin. Zooplankton in the fixed samples were later identified and enumerated. The mean biomass per animal of *Diaptomus minutus* adults, *Diaphanosoma* sp., *Bosmina* spp., and *Holopedium gibberum* was determined separately for each lake, by grouping 11–240 of the sugar-formalin-fixed animals depending on size, oven-drying the samples, and measuring dry weight.

Determinations of Grazing and Filtering Rates

Zooplankton community grazing rates and species filtering rates were measured in situ using a tracer alga, in a modification of Haney's methods (1971). Filtering rate (measured in $\mu L \cdot ind^{-1} \cdot h^{-1}$) and grazing rate ($\% \cdot h^{-1}$) are both measures of the rate of clearance of food particles from water. Filtering rate is used in this paper to refer to the feeding activities of individual animals, while grazing rate refers to the combined activity of the total zooplankton community, consistent with the usage of Haney (1973).

An important assumption in using a tracer food particle is that the tracer is sensed and ingested like other algae and seston of similar size. This assumption is probably true for filter-feeding cladocerans such as *Daphnia* which have broad size-selection capabilities (Bogdan and McNaught 1975). For *Bosmina* and *Diaptomus*, which may actively capture large or "good-tasting" food particles (Bleiwas and Stokes 1985; Vanderploeg and Paffenhofer 1985; DeMott 1986), the filtering rate extrapolated from a tracer is representative of only a limited portion of the natural seston. This was one reason we employed two tracer particles for some of our experiments. Despite these limitations, effects of satiation from high food concentrations, pH effects, and interference from blue-green algae should still theoretically be seen.

Grazing and filtering rates were measured in triplicate at subsurface (1 m) and deep (5.5–8.5 m) locations in July 1980, July 1981, and August 1981. In the first year, only community grazing rates were determined, while in 1981 both community grazing rates and species filtering rates were measured. All grazing experiments were conducted in the late afternoon and early evening in an attempt to minimize any differences due to diurnal fluctuations in filtering rate (Starkweather 1975).

Chlorella vulgaris, a small spherical cell of 3–7 μm diameter (average 5 μm), and *Cosmarium impressulum*, a larger alga of dimensions 25–28 μm by 15–17 μm by 10–12 μm were used as the tracer food particles. The algae were cultured and labelled with ^{14}C in the laboratory, following the acidification and reneutralization technique of Holtby and Knoechel (1981). *Chlorella* was used on all sampling occasions, while *Cosmarium* was employed only in one set of experiments in August 1981.

To measure in situ grazing and filtering rates, a water sample collected using a 2-L van Dorn bottle was transferred to a 2.5-L glass reagent bottle. A 1.0-mL aliquot of the tracer stock culture (*Chlorella* or *Cosmarium*) was added to the bottle, resulting in experimental tracer concentrations of 45–730 cells·mL^{-1} (0.003–0.1 μg·mL^{-1}) and 1000–10 000 dpm·mL^{-1}. The bottle was stoppered, inverted gently three times, and resuspended at the sample depth. Zooplankton were allowed to feed for 5 min at the sample depth; 5 min was expected to be less than their gut passage time (Haney 1973). The sample was then quickly pulled up and filtered through an 80-μm mesh (1980) or 112 μm-mesh (1981). Plankton retained on the mesh were immediately placed into carbonated water for 1–2 min (Burns 1969). In 1980, animals were rinsed with 150 mL of lakewater, backwashed onto a 0.4-μm Unipore filter and filtered at <15 mm Hg pressure. The filter was then transferred to a plastic-capped glass scintillation vial and 0.7 mL of 4% buffered sugar-formalin, which was sufficient to cover the filter and animals, was added to preserve the sample. In 1981, anaesthetized plankton were rinsed with 150 mL of 7-μm filtered lakewater and backwashed into a scintillation vial to which buffered sugar-formalin was added to a final concentration of 4–5%.

Filtrate that passed through the 80-μm or 112-μm mesh was collected for each replicate, and a sample added to Aquasol for radioactivity determination. Background activity counts on duplicate zooplankton and phytoplankton samples were measured on each sampling date.

Laboratory handling of zooplankton samples differed between years. In 1980 experiments when only community grazing rates were determined, the entire preserved zooplankton sample, including 0.7 mL of sugar-formalin was solubilized by adding 1.5 mL of NCS and heating the samples at 50°C in a drying oven for several days. After cooling, 0.05 mL of glacial acetic acid and 10 mL of Aquasol scintillation cocktail were added.

For 1981 experiments, sugar-formalin-preserved samples were sorted for filtering rate determinations of individual species. Individuals of *Diaptomus minutus, Diaphanosoma* sp., *Bosmina* spp. (*B. longirostris* and *E. tubicen*), and *Holopedium gibberum* were placed in separate scintillation vials. Since we were testing possible relationships with environmental variables, we attempted to keep zooplankton size relatively consistent by sorting *Bosmina* >0.4 mm, large individuals of *Diaphanosoma*, and adult or large copepodids of *Diaptomus*. For *Diaptomus* males, egg-bearing females, females without eggs, and large copepodids were at first measured separately, but one-way ANOVA (separately for each lake, depth, and date) indicated no significant differences ($p>0.05$) in filtering rate among the four groups for 18 out of 21 experiments. All *Diaptomus* were considered together in subsequent analyses. In order to achieve estimated dpm's of >100 per vial, a minimum of five individuals of *Diaptomus* and *Diaphanosoma*, and 10 *Bosmina* were grouped when possible. Since these experiments were conducted using the natural zooplankton communities, every species was not always present in each lake. A total of 1005, 261, 383, and 43 individuals of *Diaptomus minutus, Diaphanosoma, Bosmina*, and *Holopedium*, respectively were sorted for filtering rate determinations. Animals were solubilized by adding 0.5 mL of NCS to the vials, and the samples were incubated at 50°C for 1–2 d. After cooling, 10 mL OCS scintillation cocktail and 2 mL Aquasol were added.

To determine community grazing rates in 1981 experiments, preserved zooplankton samples were gently filtered onto 0.4-μm or 3.0-μm Unipore filters, transferred to scintillation vials, 1.0 mL NCS added and incubated at 50°C for 1–2 d. After cooling, 10 mL Aquasol was added.

Holtby and Knoechel (1981) demonstrated substantial losses of activity into the preservative for formalin-preserved zooplankton led ^{14}C labelled food. For the 1981 data, radioactivity of the sugar-formalin in which each zooplankton sample had been stored was measured, and dpm for each sample was corrected for the loss. Although percent loss varied considerably among samples (23–78%), the average percentage loss was 58% ($n = 107$), which agreed well with Holtby and Knoechel's estimates of 57% loss.

All samples were counted for 3–6 cycles of 2 min on Packard Tri-Carb liquid scintillation spectrometer at the ^{14}C setting and counting efficiency was measured by the internal standardization method for at least five samples from each group of samples processed.

Comparison with Haney Grazing Chamber

Several experiments were conducted to compare filtering rates measured by the a Haney grazing chamber (Haney 1971) with the present reagent bottle incubation chamber. No consistent differences were found between the two methods in the filtering rates of individual zooplankton species or community grazing rates, as indicated by a nonsignificant sign test for 20 comparisons. Grazing and filtering rates measured by the bottle incubation chamber were 46 to 216% ($\bar{x} = 106\%$) of the values measured by the Haney chamber, excluding exceptionally high and low values of 1852 and 23%.

Data Analysis

Community grazing rates were first transformed to log grazing rate in order to stabilize the variance (Sokal and Rohlf 1969). Species filtering rates were not transformed because the Kolmogov-Smirnov test indicated the distribution of values did not differ significantly from normal ($p > 0.05$).

For each zooplankton species and the zooplankton community, mean filtering rates that were calculated from the triplicate experiments were tested for correlation with 12 measured parameters, both biotic and abiotic, using a product–moment correlation. Interactions between variables were also determined by correlation analysis.

Factorial analysis of variance was employed to test for differences between tracer algae. Filtering rates were compared among lakes, depths, and tracer particles (*Chlorella* or *Cosmarium*) separately for each zooplankton species and also for the zooplankton community. SAS programs were utilized for the above analyses.

Results

Some parameters describing the study lakes individually are presented in Table 1. In general, conductivity was low, ranging between 32–63 μmho·cm^{-1} in the seven lakes. Subsurface temperatures varied from 21.8 to 26.5°C while deep temperatures ranged between 16.7 and 22.8°C. Dissolved oxygen levels at the deep sites varied between 5–11 μg·L^{-1}. These oxygen levels are not expected to limit zooplankton distribution or grazing (Ruttner 1963; Kring and O'Brien 1976b). These lakes are influenced to some extent by emissions from Sudbury's smelt-

TABLE 1. Some morphometric, physical, chemical, and biological characteristics of the study lakes. Surface area and mean depth data are from Ontario Ministry of Natural Resources lake surveys. Aluminum and manganese concentrations were taken from other studies by P. Stokes, or supplied by Ontario Ministry of the Environment (pers. comm.). Other parameters represent the mean of measurements taken in this study from May to August 1980 and 1981. Al and Mn concentrations for Daoust Lake were not available.

	Charlton	Frood	Daoust	Tyson	Carlyle	Johnnie	Ruth-Roy
Surface area (km^2)	2.2	1.9	0.6	11.4	1.5	3.9	0.5
Mean depth (m)	7.4	5.4	6.7	11.9	5.9	7.9	6.4
pH	7.1	6.7	6.5	5.6	5.4	5.1	4.6
Alkalinity ($\mu eq \cdot L^{-1}$)	89	53	69	4	−9	1	−22
Secchi disc transparency (m)	4.2	5.4	2.9	3.3	7.0	6.7	>9
Total Al ($\mu g \cdot L^{-1}$)	32	38	NA	110	150	150	490
Total Mn ($\mu g \cdot L^{-1}$)	13	19	NA	86	89	104	108
Phytoplankton biomass ($mg \cdot L^{-1}$)	1.2	0.5	1.8	0.8	0.6	0.4	0.1
Phytoplankton numbers ($Cells \cdot mL^{-1} \times 10^{-3}$)	2.9	2.6	3.1	13.0	13.0	19.2	0.6
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	1.4	1.7	2.1	3.0	1.2	1.1	0.3
Crustacean biomass ($\mu g \cdot L^{-1}$)	33	96	96	53	68	61	28
Crustacean numbers ($No. \cdot mL^{-1}$, excluding nauplii)	15	50	46	19	29	37	18
Number of grazing experiments	6	6	2	2	4	6	4

TABLE 2. Correlation of species filtering rate and community grazing rate with several biotic and abiotic variables. *R* values are presented, with significant correlations ($p<0.05$) indicated by *, and highly significant correlations ($p<0.01$) indicated by **. *Chlorella* was used as the tracer particle for these experiments.

	Diaptomus	*Diaphanosoma*	*Bosmina*	*Holopedium*	Zooplankton community
pH	−.61**	−.69**	−.27	−.65[d]	−.06
Alkalinity	−.66**	−.65*	−.34	−.74*	−20
Temperature	.56*	.41	.09	.15	−.20
Light transmission	.55*	.33	.12	.13	−.13
Edible seston biomass[a]	−.44	.14	−.08	.09	−.18[e]
Edible phytoplankton biomass[b]	−.49*	−.11	−.10	−.24	−.11
Total phytoplankton biomass	−.57*	−.38	−.25	−.49	−.01
Non bluegreen nanoplankton biomass[c]	.30	−.22	−.15	−.15	−.11
Phytoplankton numbers	−.03	.46	−.10	.56	−.04
Percentage blue-greens	−.13	.44	−.04	.53	−.11
Chlorophyll *a* concentration	−.38	−.24	.14	−.28	.59**
Animal weight	−.59**	.40	.36	—	—
Number of experiments	18	13	14	9	30

[a]Edible seston biomass was defined as phytoplankton and detrital particles <30 μm maximum dimension.

[b]Edible phytoplankton biomass consisted of phytoplankton <30 μm.

[c]Nonblue-green nanoplankton biomass was defined as phytoplankton <15 μm, excluding blue-green algae.

[d]$p<.1$.

[e]$n = 20$.

ers, and copper and nickel levels were slightly elevated (2–5 ppm copper and 5–22 ppm nickel; Ontario Ministry of the Environment, pers. comm., other studies by P. Stokes). More detailed information regarding zooplankton and phytoplankton distribution in these lakes is presented by Bleiwas (1983) and Bleiwas et al. (1984).

Filtering rates varied considerably among experiments, ranging over two orders of magnitude for some species. Average filtering rates measured using *Chlorella* as the tracer cell were 148, 248, 38, and 855 $\mu L \cdot ind^{-1} \cdot h^{-1}$ for *Diaptomus*, *Diaphanosoma*, *Bosmina*, and *Holopedium* respectively, with coefficients of variation ranging from 11 to 112% among the three replicates.

Filtering rates of each species were tested for correlation with several environmental parameters (Table 2; Fig. 1). Inter-relationships among environmental variables are presented in Table 3. The filtering rates of *Diaptomus* and *Diaphanosoma* were significantly negatively correlated with pH and alkalinity, and the same trend was observed for *Holopedium*. The filtering rate of *Bosmina*, on the other hand, was not correlated with pH or alkalinity.

Measured characteristics of the phytoplankton food source were significantly correlated with filtering rate only for *Diaptomus* (Table 2). Edible and total phytoplankton biomass were negatively correlated with *Diaptomus* filtering rate.

Since filtering rate was associated with temperature and light intensity for *Diaptomus* (Table 2), the data were separated into subsurface and deep experiments in order to compare filtering rates among experiments which were similar in temperature.

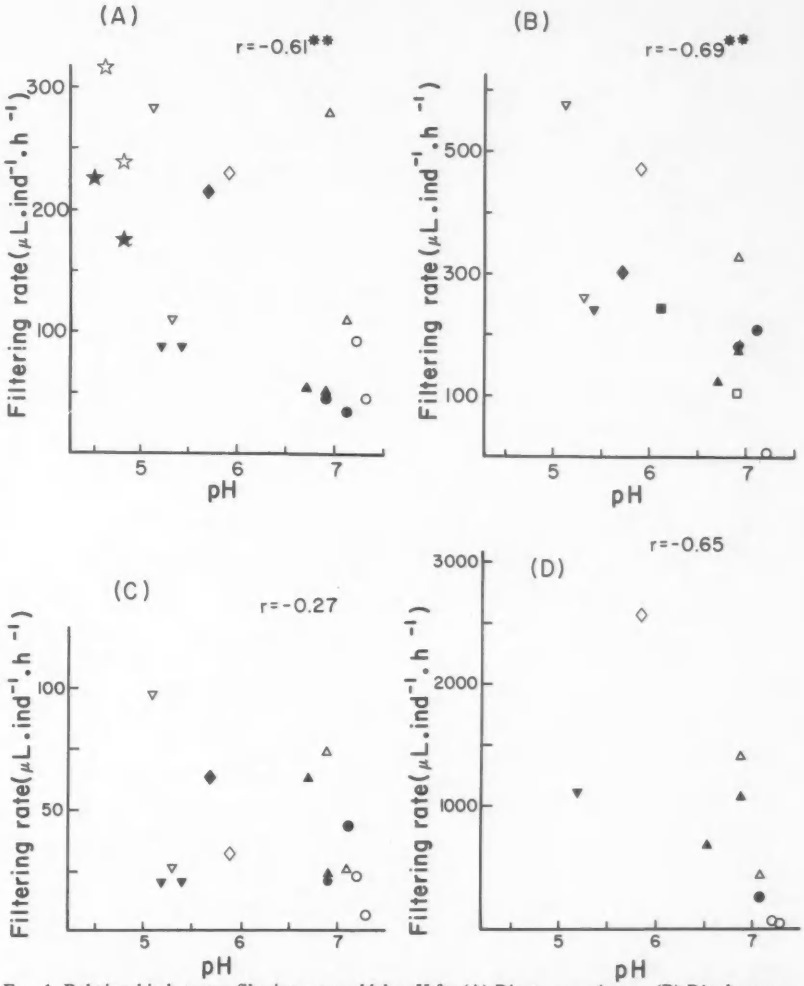

FIG. 1. Relationship between filtering rate and lake pH for (A) *Diaptomus minutus*, (B) *Diaphanosoma* sp., (C) *Bosmina* spp., and (D) *Holopedium gibberum*. Open symbols represent subsurface experiments and closed symbols represent deep experiments. The lakes are shown as ○ Charlton, Δ Frood, □ Daoust, ◇ Carlyle, ∇ Johnnie, ☆ Ruth-Roy. *Chlorella* was the tracer alga.

Separate analysis of subsurface and deep experiments indicated no significant correlation with temperature ($p>0.1$) or with edible phytoplankton biomass (which was correlated with temperature, Table 3). The association of filtering rate with pH was maintained ($p<0.1$).

Filtering rate was expected to be positively correlated with zooplankton biomass (Burns 1969). For *Diaphanosoma* and *Bosmina*, the relationship was in the anticipated direction, although the correlation was not significant ($p>0.05$). Contrary to expectation, *Diaptomus* filtering rate was negatively correlated with its biomass (Table 2). *Diaptomus* biomass was also correlated with lake pH, alkalinity, and total phytoplankton biomass (Table 3).

Filtering rates standardized for zooplankton biomass ($\mu L \cdot \mu g$ zooplankton dry weight$^{-1} \cdot h^{-1}$) were also calculated. Average biomass corrected filtering rates for *Diaptomus*, *Diaphanosoma*, *Bosmina*, and *Holopedium* were 69, 136, 37, and 115 $\mu L \cdot \mu g^{-1} \cdot h^{-1}$, respectively. Factors that were significantly correlated with filtering rate (in $\mu L \cdot ind^{-1} \cdot h^{-1}$) were also correlated with biomass corrected filtering rate. Correlation of biomass corrected filtering rate with pH yielded r values of -0.70 ($p<0.01$) for *Diaptomus*, -0.62 ($p<0.05$) for *Diaphanosoma*, -0.30 (NS) for *Bosmina* and -0.65 ($p<0.1$) for *Holopedium*.

Zooplankton Community Grazing Rates

Grazing rates measured with the tracer *Chlorella* varied considerably among experiments, with a range from 0.2–6.5%·h^{-1} (5–155%·d^{-1}). Community grazing rate was tested for correlation with a number of biotic and abiotic variables (Table 2). The only significant correlation was with chlorophyll concentration. Closer inspection of the relationship between community grazing rate and chlorophyll *a* concentration revealed that it could be attributed to extremely high chlorophyll concentra-

TABLE 3. Pairwise correlation coefficients among abiotic and biotic variables. Significant correlations ($p<.05$) were indicated by *, highly significant correlations ($p<.01$) by **. All parameters except animal biomass were measured at subsurface and deep locations in July and August 1981. Animal biomass measurements represent an average value for each lake, and were tested for correlation with average values for pH, alkalinity, total phytoplankton biomass, phytoplankton numbers, and chlorophyll *a* concentration for each lake.

	pH	Alk.	Temp.	Light trans.	Edible Seston bio.	Edible Phyto bio.	Total Phyto bio.	Non-bg nano bio.	Phyto number	Percent blue-green	Chl *a* conc.	*n*
pH	—											20
Alkalinity	.94**	—										18
Temperature	−.13	−.20	—									20
Light transmission	−.06	−.15	.75**	—								20
Edible seston biomass	.29	.33	−.52*	−.55*	—							20
Edible phytoplankton biomass	.53*	.58*	−.49*	−.42	.84**	—						20
Total phytoplankton biomass	.70**	.72**	−.36	−.31	.68	.93**	—					20
Nonblue-green nanoplankton biomass	.48*	.47	−.13	−.24	.54*	.69**	.71	—				20
Phytoplankton numbers	−.26	−.19	−.09	−.24	.56**	.25	−.02	.21	—			20
Percentage blue-greens	.03	.20	−.26	−.11	.51*	.27	.08	.10	.58**	—		20
Chlorophyll *a* concentrations	.39	.52*	−.62**	−.32	.47*	.70**	.67**	.46*	.11	.27	—	19
Diaptomus biomass	.84*	.84*	—	—	—	—	.99**	—	−.17	—	.61	5
Diaphanosoma biomass	−.05	.14	—	—	—	—	.48	—	−.53	—	−.03	6
Bosmina biomass	−.18	−.34	—	—	—	—	.00	—	−.11	—	.37	5
Holopedium biomass	.08	.19	—	—	—	—	.71*	—	−.03	—	.54	6

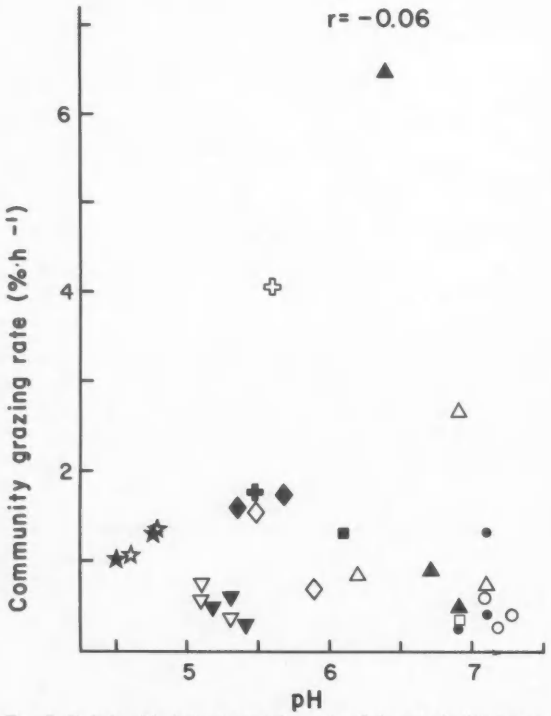

FIG. 2. Relationship between grazing rate of the zooplankton community and lake pH. Symbols as for Fig. 1, with the addition of Tyson L. (✚). *Chlorella* was the tracer alga.

tions encountered in only two out of 30 experiments. Chlorophyll concentrations in these samples were 4.3–4.4 $\mu g \cdot L^{-1}$, compared with 0.2–3.1 $\mu g \cdot L^{-1}$ at other sites, and grazing rates for the two experiments were 4.1–6.5% $\cdot h^{-1}$ while grazing rates at other sites ranged between 0.2–2.7% $\cdot h^{-1}$. Excluding these two experiments from the correlation yielded an r value of −0.11 ($p>0.05$). The unusually high grazing rates may have occurred because the zooplankton migrated to the stratum of highest food concentration, perhaps representing grazing rates at chlorophyll peaks.

Zooplankton community grazing rate was not correlated with pH (Fig. 2).

Comparison of Filtering Rates Measured Employing *Chlorella* and *Cosmarium* as Tracer Particles

Filtering rates measured using *Cosmarium impressulum* as the tracer frequently differed from those determined using *Chlorella vulgaris* (Fig. 3). Results from an ANOVA (Lake by Depth by Tracer for each species) indicated that the tracer used significantly affected the filtering rates of *Bosmina*, *Diaphanosoma*, and *Diaptomus*, as well as zooplankton community grazing rate ($F=57.8$, $p<0.00001$; $F=48.8$, $p<0.0001$; $F=12.2$, $p<0.001$; $F=16.0$, $p<0.001$, respectively). *Holopedium* was not included in this analysis because too few animals were measured.

The filtering rate of *Bosmina* was on the average six times higher when measured using the larger alga *Cosmarium* than the smaller *Chlorella* (Fig. 3, Bleiwas and Stokes 1985). In contrast, the filtering rate of *Diaphanosoma* was generally higher when measured using *Chlorella* than *Cosmarium*. For both species, the effect of the tracer was greater than the influence of lake or depth. *Diaptomus* filtering rate was influenced by the tracer employed, but the effect of tracer was not consistent among lakes (Fig. 3).

As might be expected from the complex responses of individual species to the tracer particles, measured community grazing rate was influenced by the tracer particle employed, but the response differed among experiments. Significant differences ($p<0.05$) between grazing rates measured utilizing *Chlorella* and *Cosmarium* were present for Frood and Johnnie subsurface experiments. There was never any indication that the size of *Cosmarium* prevented grazing by the zooplankton community in acidic or circumneutral lakes (Fig. 3).

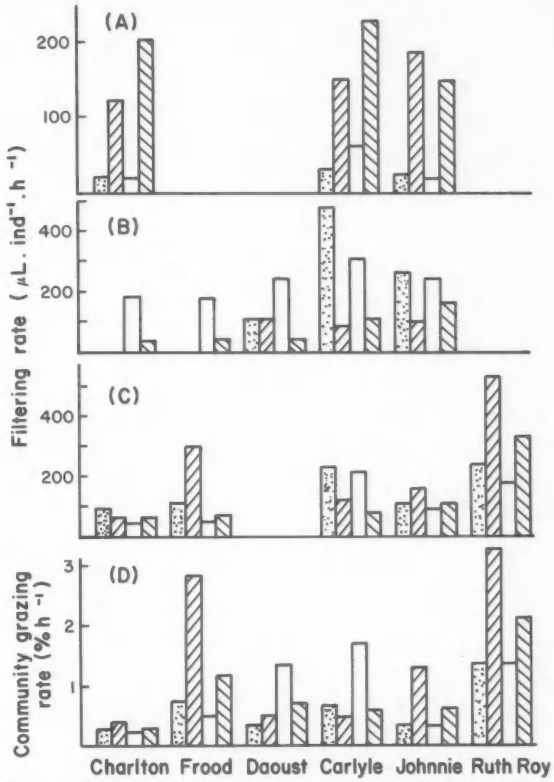

FIG. 3. Filtering and grazing rates comparing *Chlorella vulgaris* and *Cosmarium impressulum* as tracer particles for (A) *Bosmina* spp., (B) *Diaphanosoma* sp., (C) *Diaptomus minutus*, and (D) zooplankton community. Experiments are represented as ▩ subsurface *Chlorella* tracer, ▨ subsurface *Cosmarium* tracer, □ deep *Chlorella* tracer, ▧ deep *Cosmarium* tracer.

Despite differences between filtering rates measured using *Chlorella* and *Cosmarium*, trends of filtering rate with pH were similar for each tracer. Correlation of filtering rate with pH measured using *Cosmarium* yielded r values of -0.54 ($p<0.1$, -0.57 ($p<0.1$), -0.03 (NS) and 0.10 (NS) for *Diaptomus*, *Diaphanosoma*, and *Bosmina* filtering rates and zooplankton community grazing rates, respectively.

Discussion

Filtering Rates of Individual Species

Filtering rates measured in the present investigation were consistent with rates reported from several previous field studies. Filtering rates of *Diaptomus minutus* have been reported to be between 2–410 $\mu L \cdot ind^{-1} \cdot h^{-1}$ (Bodgan and McNaught 1975; Chow-Fraser 1986). The filtering rate of *Diaphanosoma* was between 0–212 $\mu L \cdot ind^{-1} \cdot h^{-1}$ (Haney 1973; Buckingham 1978; Janicki 1980). *Bosmina* was reported to feed at a rate of 0.4–480 $\mu L \cdot ind^{-1} \cdot h^{-1}$ (Haney 1973; Janicki 1980; DeMott 1982; Knoechel and Holtby 1986a). Previous studies on *Holopedium* have found filtering rates of 0–4979 $\mu L \cdot ind^{-1} \cdot h^{-1}$ (Buckingham 1978; Haney 1985).

In the present study, high filtering rates were associated with low lake pH and alkalinity for *Diaptomus*, *Diaphanosoma*, and *Holopedium*, but not for *Bosmina* (Table 2, Fig. 1). Although changes in the pH to which individual zooplankters are exposed can cause decreased filtering rates (Kring and O'Brien 1976a; Janicki 1980), the animals in the present study were presumably acclimated to ambient conditions of pH as well as other factors since the experiments were conducted in situ.

The correlation between filtering rate and pH for *Diaptomus*, *Diaphanosoma*, and *Holopedium* may reflect a direct relationship (i.e. low pH may have caused the high filtering rates), or may result from the relationship of filtering rate with other parameters correlated with pH. Although the present experimental design does not differentiate between effects of pH per se and pH-related differences, some insight into possible relationships may be gained by examining factors which have been shown to influence filtering rate in other studies.

Filtering rate increases exponentially with increasing zooplankton length (Burns 1969; Chow-Fraser and Knoechel 1985; Haney 1985). We attempted to keep zooplankton size uniform among experiments in order to detect relationships with environmental variables such as pH, but this was not always possible. Consequently, zooplankton biomass, which increases with length (Rosen 1981), was determined to estimate the effect of zooplankton sizes in various lakes. The filtering rates of *Diaphanosoma*, *Bosmina*, and *Holopedium* were not significantly correlated with biomass, but contrary to our expectations, *Diaptomus* filtering rate was negatively correlated with biomass (Table 2). Zooplankton biomass in these experiments was averaged for each lake rather than measured for the individual animals whose filtering rates were determined, thus the expected relationship between biomass and filtering rate may have been confounded by other factors. Both filtering rate and biomass of *Diaptomus* were correlated with several other variables (i.e. temperature, phytoplankton biomass, pH, see Tables 2, 3), and the negative correlation probably reflects relationships with these other variables. These results suggest that the association between *Diaphanosoma* and *Holopedium* filtering rates and pH in this study did not result from pH-related size differences in the zooplankton. This interpretation is consistent with trends observed for biomass-corrected filtering rates: biomass-corrected filtering rates for *Diaphanosoma*, *Holopedium*, and *Diaptomus* were negatively correlated with pH.

Diaptomus biomass was highly significantly correlated with total phytoplankton biomass ($r=0.99$, $n=5$, see Table 3). This suggests that individual *Diaptomus minutus* may grow larger in lakes with more food; in these data, however, there was no correlation between *Diaptomus* biomass and phytoplankton number. These values represent average values for only five lakes, and more measurements would be needed before any such conclusions could be drawn.

Food concentration, particle size, and food quality may be important in determining zooplankton filtering rates (McMahon and Rigler 1965; Porter et al. 1982; Richman and Dodson 1983; Peters and Downing 1984; Chow-Fraser 1986; DeMott 1986; Knoechel and Holtby 1986b). To test the importance of these factors we measured the concentration of food naturally available to herbivorous zooplankton using several parameters: edible seston biomass (<30 μm), edible phytoplankton biomass (<30 μm), biomass of nanoplankton (<15 μm) excluding blue-greens, total phytoplankton biomass, phytoplankton numbers, and chlorophyll *a* concentration. If food concentrations were above the incipient limting level for a given species (McMahon and Rigler 1965), a decrease in

filtering rate with increasing food concentration may be expected. This might result in a negative correlation between filtering rate and pH, as edible and total phytoplankton biomass were positively correlated with lake pH (Table 3). However there was no significant correlation between any measure of food concentration and filtering rate for *Diaphanosoma*, *Bosmina*, and *Holopedium* (Table 2, 3). No threshold concentration was evident from visual examination of plots of filtering rate versus food concentration. Edible seston concentrations in these oligotrophic lakes (0.2–3.2 $mg \cdot L^{-1}$ wet weight) may have been too low to inhibit filtering for these species. The association of *Diaphanosoma* and *Holopedium* filtering rate with pH was thus not a reflection of an underlying relationship between filtering rate and food concentration. The filtering rate of *Diaptomus* was, however, significantly correlated with some measures of food concentration. Low food concentrations in the acidic lakes might be important in promoting high filtering rates of *Diaptomus*. Further study is needed to clarify the relationships involved.

It is possible that testing food concentration without regard to its composition could misrepresent actual food availability since some blue-green algae may be filtered more slowly than other algae (Arnold 1971), or may be rejected altogether, causing a pause in filtering activity (Burns 1968b). If high levels of blue-green algae were depressing filtering rates in some of the experiments, then a negative correlation between percentage blue-greens and filtering rate would be expected. This was not observed for any of the zooplankton species studied, despite the fact that blue-greens made up as much as 95% of phytoplankton biomass in some experiments.

In addition to biotic factors, abiotic factors could also influence zooplankton filtering rates. Increases in water temperature to 20–25°C have been shown to increase filtering rates in laboratory studies (Burns 1969; Kibby 1971) but not in some field experiments (Chow-Fraser 1986; Knoechel and Holtby 1986a,b). Although experimental temperatures did not vary greatly in the present study (range of 17–24°C), *Diaptomus* filtering rates were positively correlated with temperature and light transmission. The filtering rates of *Diaphanosoma*, *Bosmina*, and *Holopedium* were not associated with temperature.

Possible effects of metals must also be considered, as elevated metal concentrations are often associated with low pH lakes (Haines 1981), and high levels of toxic substances may depress filtering rates (Cooley 1977). Indeed, concentrations of some metals were higher in the acidic study lakes than in the circumneutral lakes studied (Table 1). However filtering rates increased with decreasing pH, or remained unchanged, which is contrary to expectations if elevated metal levels were affecting filtering rate.

None of the parameters tested in the present study were useful in explaining the negative correlation between *Diaphanosoma* and *Holopedium* filtering rates and pH. The filtering rates of these species were not associated with zooplankton biomass, food concentration, food quality, or temperature, factors which represent the major determinants of filtering rates reported in the literature. Although it is possible that some unmeasured correlate of pH caused the relationship between filtering rates and pH, a more probable explanation is that pH has a direct effect on the filtering rate of *Diaphanosoma* and *Holopedium*.

The negative correlation between *Diaptomus* filtering rate and pH may have been caused by the low food concentration found in the acidic lakes. Alternatively, pH per se (or an unmeasured correlate of pH) may have affected the filtering rate of *Diaptomus*, and the observed correlation with food concentration reflected this relationship. Further studies examining the influence of pH, food concentration, and food quality separately and in combination on the filtering rates of *Diaptomus*, *Diaphanosoma*, and *Holopedium* are required to understand the causes of correlations observed in these in situ experiments.

In contrast to the trends for *Diaptomus*, *Diaphanosoma*, and *Holopedium*, the filtering rate of *Bosmina* was uncorrelated with lake pH between 5.1 and 7.3. This is consistent with the results of Janicki (1980) who observed the filtering rate of *Bosmina longirostris* was not related to ambient pH. Janicki also transferred animals from water of pH 6.6 to pH 4.8 and observed no alteration in the filtering rate of *Bosmina* whereas filtering rates of *Diaptomus*, *Diaphanosoma*, and *Daphnia* declined at the new pH. The consistent filtering activity of *Bosmina* over a wide range of ambient pH's and considerable declines in pH may play a role in its success in acidic waters.

Community Grazing Rates

Zooplankton community grazing rates were uncorrelated with lake pH in this study (Table 2, Fig. 1). Comparisons of grazing rates reported in the literature are consistent with this observation. Mean summer grazing rates in several nonacidic lakes varying considerably in trophy and geographical location were 0.2, 0.4, 0.9, 3.0, 0.9–2.2, and 0.5–6.7% $\cdot h^{-1}$ (Haney 1973; Gulati 1975; Gulati et al. 1982; Haney 1973; Thompson et al. 1982; and Lampbert and Taylor 1984, respectively). These are in the same range as the mean grazing rates of 0.5–4.1% $\cdot h^{-1}$ found in acidic LaCloche lakes in the present study and 2.4% $\cdot h^{-1}$ in Drowned Bog Lake measured by Haney (1973).

These data do not support the hypothesis of Yan and Strus (1980) that zooplankton community grazing rates are reduced at low pH. To clarify this discrepancy, we reexamined the calculations of Yan and Strus (1980) regarding zooplankton community grazing rates in an acidic metal-contaminated lake. Their hypothesis appears reasonable for Clearwater Lake. Filtering rates of the dominant grazer in that lake, *Bosmina longirostris*, were unchanged at low pH, and the low abundance of zooplankton combined with filtering rates which were largely unrelated to lake pH probably resulted in low community grazing rates. However this calculation should not be extrapolated to acidic lakes which do not have low zooplankton abundance and are not *Bosmina* dominated. Caution should also be used in applying the hypothesis to lakes that are acidic but not metal-contaminated.

Since community grazing rate was observed to be unrelated to lake pH, it is unlikely that changes in total grazing pressure caused systematic alterations in phytoplankton community structure or biomass in acidic lakes. However this does not rule out the possibility that grazing pressure on specific size categories or taxa of the phytoplankton was more or less intensive at low pH than in circumneutral lakes. Some indication of grazing pressure on small versus large cells can be gained from a comparison of community grazing rates on *Chlorella* and *Cosmarium*.

We did observe significant differences between community grazing rates on the small *Chlorella* and the larger *Cosmarium*, and community response depended in part on the lake examined (Fig. 3). However there was no indication that this differential grazing pressure was related to lake acidity. Community graz-

ing rates were higher on *Cosmarium* than *Chlorella* in acidic Johnnie and Ruth-Roy lakes as well as in circumneutral Frood lake, while *Chlorella* appeared to be more actively grazed in some experiments in acidic Carlyle and circumneutral Daoust lakes. There was no evidence that grazing pressure on large cells was reduced in the acidic lakes.

In summary, the filtering rates of *Diaptomus*, *Diaphosoma*, and *Holopedium* were negatively correlated with lake pH, whereas *Bosmina* filtering rate was uncorrelated with pH. Although many of the major environmental parameters that have been found to influence zooplankton filtering rate were considered, they did not explain the observed correlations. Zooplankton community grazing rate was also uncorrelated with lake pH. This study, conducted with the zooplankton communities present during the experiments, is limited to the species, numbers and environmental conditions encountered. Further studies under more controlled conditions may be useful in unravelling the causes behind the correlations or lack of correlations observed in the present investigation.

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Soft-Bodied Zooplankton Predators and Competitors of Larval Herring (*Clupea harengus pallasi*) at Herring Spawning Grounds in British Columbia[1]

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Purcell, J. E. 1990. Soft-bodied zooplankton predators and competitors of larval herring (*Clupea harengus pallasi*) at herring spawning grounds in British Columbia. Can. J. Fish. Aquat. Sci. 47: 505–515.

The soft-bodied zooplankton predators and the microzooplankton foods of herring larvae were collected at 28 herring spawning grounds in British Columbia in April 1984, when herring larvae (*Clupea harengus pallasi*) hatched. The same predator species were found throughout coastal B.C., but total densities varied over three orders of magnitude. Barkley Sound had the highest densities, and bays in northern B.C. and the Strait of Georgia had higher densities than open shorelines in both regions. Eight of 18 species of soft-bodied predators contained herring larvae. The hydromedusan *Aequorea victoria* was the most important predator, and consumed 0.4% of the herring larvae·d^{-1} in Fanny Bay, and 12.5, 3.9, and 0%·d^{-1} over three consecutive days in Kulleet Bay as larval densities decreased. Herring larvae ate copepod nauplii (84.4%) and other microzooplankton. Densities of these prey varied between 0.8 and 37·L^{-1} among 21 locations sampled. Only three species of hydromedusae showed extensive dietary overlap (90–100%) with larval herring. Soft-bodied predators consumed <1%·d^{-1} of the microzooplankton in 17 locations, and could have affected densities in only one of the 21 locations. The ratios of microzooplankton to predator densities varied over 1000-fold, suggesting great differences in the chances for herring larval survival among various locations.

Les prédateurs de zooplancton à corps mou et le microzooplancton dont se nourrissent les larves de hareng ont été prélevés dans 28 aires de fraie du hareng en Colombie-Britannique en avril 1984, au moment de l'éclosion des larves de hareng (*Clupea harengus pallasi*). Les mêmes espèces prédatrices ont été observées tout le long de la côte de la Colombie-Britannique, mais les densités totales variaient de trois ordres de grandeur. C'est dans le détroit Barkley que 'on a observé les plus fortes densités, les baies du nord de la province et le détroit de Georgie affichant des densités supérieures à celles des côtes ouvertes des deux régions. Huit des 18 espèces de prédateurs à corps mou contenaient des larves de hareng. Le prédateur le plus important, l'hydroméduse *Aequorea victoria* consommait 0.4 % de larves de hareng d·$^{-1}$ dans la baie Fanny, et 12.5, 3.9, et 0 %·d^{-1} pendant trois jours consécutifs dans la baie Kulleet, à mesure que la densité des larves décroissait. Les larves de hareng se nourrissaient de copépodes nauplii (84.4 %) et d'autres microzooplanctons. Les densités de ces proies variaient de 0.8 à 37·L^{-1} dans les 21 endroits échantillons. Seules trois espèces d'hydroméduse avaient un régime alimentaire qui chevauchait largement (90–100 %) celui des larves de hareng. Les prédateurs à corps mou consommaient plus de 1 %·d^{-1} de microzooplancton dans 17 endroits et pourraient avoir influé sur les densités dans seulement un endroit sur les 21. Les ratios de densité de microzooplancton par prédateur variaient de plus de 1000, ce qui laisse croire à de grandes différences dans les chances de survie des larves de hareng en divers endroits.

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Pelagic cnidarians, ctenophores, and chaetognaths are potentially both predators of larval fishes and competitors with them for food. Many soft-bodied predators consume fish eggs and larvae (reviewed in Alvariño 1984; Purcell 1985), however, their principal prey are zooplankters (Purcell 1985). The possible additional importance of these predators as competitors for food with fish larvae often has been suggested (e.g. Lebour 1922, 1923; Sveshnikov 1963; Purcell 1985), but seldom explored. Laboratory data by Sveshnikov (1963) on feeding of the hydromedusae *Sarsia tubulosa*, *Bougainvillia supercilliaris*, *Rathkea octopunctata*, and *Perigonimus yoldia-arcticae* from the White Sea, USSR indicated that the hydromedusae could eat herring (*Clupea harengus pallasi*) larvae. However, other zooplankton that the hydromedusae ingested were not the foods of herring or their larvae, so there was no further evidence of their impact on herring survival. Möller (1980) estimated that the scyphomedusa *Aurelia aurita* consumed 4.4%·d^{-1} of the herring larvae in 1979 and 2.6%·d^{-1} in 1980 in Kiel Bight, Germany. Diets of the medusae and herring larvae overlapped, but Möller did not quantify their feeding on zooplankton to evaluate whether foods of the larvae might be reduced. Frank (1986) estimated that average predation of the crustacean zooplankton standing stocks on Browns Bank off Nova Scotia, Canada by the ctenophore *Pleurobrachia pileus* was 8.8%·d^{-1} in 1983 and 0.7%·d^{-1} in 1984. He felt that this would limit the copepod eggs and nauplii available to the fish larvae present. Fish eggs occurred in <2% of the 600 *P. pileus* examined and no fish larvae were seen in the guts. Therefore, reduction of larval foods was the most likely effect of *P. pileus* on larval fishes.

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Starvation and predation are thought to be the two major causes of mortality in fish larvae (Leggett 1986). The present study was undertaken to examine predation and competition for food between soft-bodied zooplankton and recently-hatched herring larvae in 28 locations throughout coastal British Columbia in April 1984.

Materials and Methods

Plankton Collection

In 1984, 28 locations were sampled that had been consistently used for spawning by herring in British Columbia (Haegele and Fitzpatrick 1983) (Figs. 1 and 2). Plankton samples were collected in April as near to the time herring larvae hatched as possible. Herring larvae hatch in about 14 d when incubated at 9.0–10.5°C, and in about 21 d at 5.5–8.5°C, and exhaust their yolk reserves within 6 d (Alderdice and Velsen 1971). Plankton samples provided data on densities of crustacean zooplankton, fish larvae, and soft-bodied predators. One or two stations were sampled at each location except in Kulleet Bay (No. 7) and in Baynes Sound (No. 5) where three and four stations were sampled, respectively. At each station, replicated zooplankton collections were made at 1 and 5 m depth with a 333-μm mesh, 0.75 m diameter conical net equipped with a flowmeter. The net was towed horizontally at 1 to 1.5 knots for 3 min, or as little as 1 min when necessary to prevent clogging. The volumes filtered in locations No. 6, 7, and 10 averaged 15.0 ± 5.6 m^3, whereas those at all other locations averaged 35.8 ± 10.3 m^3. After each tow, the net was rinsed thoroughly into the cod end with sea water. Formaldehyde buffered with sodium borate was added to the samples to bring the final concentration to 5% formalin. Sampling was restricted to the surface 5 m for accuracy in determining predation rates (Purcell 1989).

In the laboratory, large medusae were removed from the samples and counted. Then the plankton samples were subsampled with a Folsom plankton splitter, and all specimens of each taxonomic group counted from one or more subsamples. All medusae were removed from half or whole samples and identified to species. Fish larvae other than herring were identified to family, and crustacean zooplankton identified to order. Densities of the plankton organisms are expressed as their mean number·m$^{-3} \pm$ standard deviation (SD) for all tows at a location.

In order to determine the densities of *Aequorea victoria* and *Phacellophora camschatica* and to detect the presence of delicate species like the ctenophore *Bolinopsis infundibulum*, 1-m diameter, 1600-μm soft nylon mesh conical net fitted with a flowmeter was towed for 5 or 10 min, filtering an average of 123.5 ± 30.0 m^3 or 282.8 ± 67.9 m^3, respectively. One tow was made at each station at 1 and at 5 m depths.

Diameters of all preserved *Aequorea victoria* from selected plankton tows in 1983 (Purcell 1989) and 1984 were measured with a millimeter rule under a petri dish, where medusae were placed subumbrellar surface down. Displacement volumes were measured in graduated cylinders, with small volume changes measured by graduations in a syringe.

Microzooplankton was sampled with a 0.5-m diameter, 63-μm mesh conical plankton net that was dropped to 5 m depth and retrieved, filtering 2 m^3 of water. One sample was taken at each station except when weather conditions prevented vertical sampling. In the laboratory, these formalin-preserved samples were diluted with sea water to 1-L volume and all zooplankton counted in three to five subsamples (each containing >50 organisms) taken with 5 or 10 mL Hensen stempel pipettes.

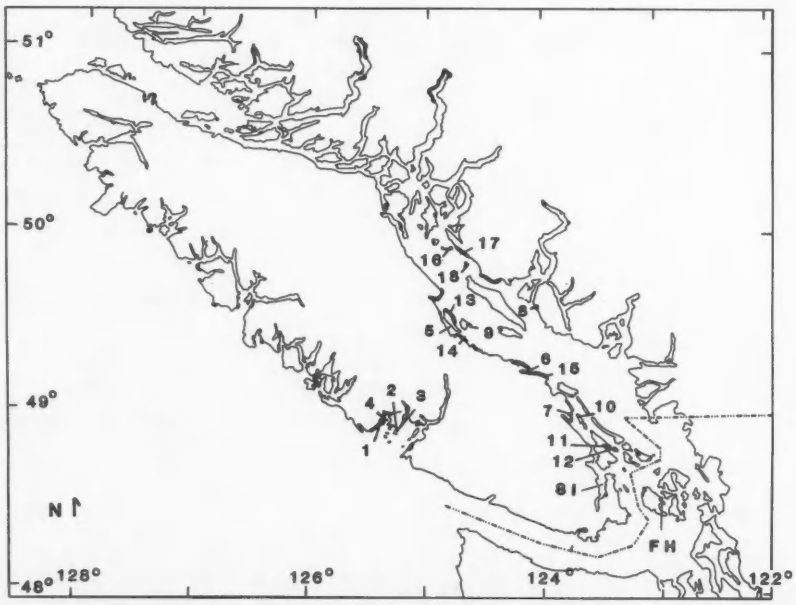

FIG. 1. Herring spawning grounds (darkened areas) and locations sampled off the coast of Vancouver Island and the southern British Columbia mainland. The numbered locations are named in Table 1. Saanich Inlet (SI), Friday Harbor, Washington (FH). Map modified from Hourston (1981).

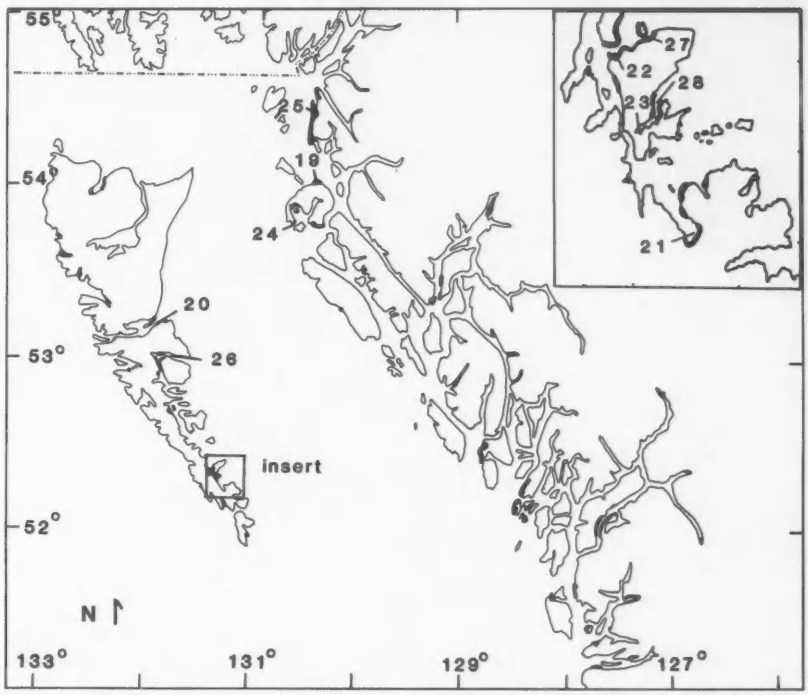

FIG. 2. Herring spawning grounds (darkened areas) and locations sampled off the coast of the Queen Charlotte Islands and the northern British Columbia mainland. The numbered locations are named in Table 1. Map modified from Hourston (1981).

Dietary Analysis

For gut content analysis, large medusae (*Aequorea victoria* and *Phacellophora camtschatica*) were collected individually and immediately preserved in 5% buffered formaldehyde solution as described in Purcell (1989). The guts of small medusae, ctenophores, and chaetognaths from the 333-μm mesh plankton samples were examined for herring larvae and other prey organisms (Purcell 1989). The number of prey consumed per day by soft-bodied predator species was calculated from the numbers of prey in the gut divided by the digestion time and multiplied by 24 h, assuming constant feeding over 24 h. Digestion times used in the calculations were as follows: *Aequorea victoria* digested herring larvae in 3.5 h and copepods in 5.4 h at 9°C (Purcell 1989). At 12–14.5°C, *Phialidium* spp. digested euphausiid eggs and nauplii in 5.6 and 3.9 h, respectively (Larson 1985). A digestion time of 4 h was assumed for other hydromedusa species in the absence of data. Digestion of copepods required 3.5 h by *Pleurobrachia bachei* (Larson 1985). A digestion time of 5 h for copepods was assumed for *Phacellophora camtschatica*, based on rates for *Aurelia aurita* (Möller 1980).

The gut contents of post yolksac herring larvae were identified and counted under a dissecting microscope at 8–35× magnification. The standard length (SL, snout to end of notochord) of larvae was measured with an ocular micrometer on the dissecting microscope.

Results

Herring Larvae

Table 1 shows the locations in which herring spawned in 1984. No spawning occurred in Nanoose Bay or Toquart Bay, which had supported important fisheries in preceding years. Larvae originating at Qualicum and nearby Comox Bluff are transported by currents into Baynes Sound, where spawning usually does not occur but where numerous larvae are found (D.E. Hay, pers. comm.). Similarly, spawning occurred near locations No. 8, 15, 17, and 27.

Herring were the predominant fish larvae in all locations where a recent spawn had occurred (Table 1). High numbers of herring larvae, and high percentages of yolksac larvae resulted from sampling during the period of hatching (locations No. 1, 2, 3, 13, 19, 24, 25; Table 1).

Predators

The same species of soft-bodied zooplankton predators (hydromedusae, ctenophores, chaetognaths, and siphonophores) occurred at sampling locations along 800 km of British Columbia coast (Tables 2 and 3). Hydromedusae generally were the most numerous of these groups, with densities exceeding $50 \cdot m^{-3}$ in 6 locations (Table 2), and *Phialidium gregarium*, *Sarsia tubulosa*, and *Rathkea octopunctata* were the most numerous species (Table 3). Ctenophores (*Pleurobrachia bachei*), chaetognaths (*Sagitta* sp.), and siphonophores (*Muggiaea atlantica*) were numerous only in Barkley Sound and the head of Poole Inlet (Table 2). *Bolinopsis infundibulum* often was collected at open water locations, but densities of this delicate ctenophore could not be determined accurately with nets, and only presence is reported. The head of Poole Inlet was the only location where the scyphomedusa *Phacellophora camschatica* was collected (densities = 1 medusa·25 m^{-3}).

TABLE 1. Dates of herring spawning at 28 locations in British Columbia in 1984, sampling dates and surface water temperatures, and densities (No.·m^{-3} ± SD) of herring larvae measured near the time of hatching, the percentages of all fish larvae that were herring, and the percentages of herring larvae that were yolksac stage. Numbers in parentheses after sampling dates are the number of days since spawning. — = no spawn.

Sampling	Locations	Spawning dates	Sampling dates in April	Temperature (°C)	Herring larvae (No.·m^{-3})	Herring larvae (% of fish species)	Herring larvae (% Yolksac larvae)
Barkley Sound	1. Forbes Island	Mar. 13–16	1 (16–19)	9.5	631.6 ± 715.8	99.3	94.8
	2. Prideaux Island	Mar. 13–16	1 (16–19)	9.5	431.6 ± 299.1	98.6	97.7
	3. Nettle Island	Mar. 13–16	1 (16–19)	9.5	197.3 ± 150.0	98.7	91.8
	4. Toquart Bay	—	1	9.5	0.4	25.0	26.5
Strait bays	5. Baynes Sound	—	6–7	9.0	32.7 ± 26.8	95.1	1.3
	6. Nanoose Bay	—	8	9.5	0.3 ± 0.3	6.4	0
	7. Kulleet Bay	Mar. 22–25	9–11 (18–21)	9.0	20.9 ± 24.4	92.1	32.8
	8. Bargain Bay	—	4	10.5	0	0	0
	9. Tribune Bay	Mar. 9, 15	5 (21,27)	9.0	63.5 ± 63.4	81.6	1.8
	10. North Cove	—	8	9.0	4.8 ± 3.7	94.6	8.1
	11. Long Harbor	—	3	9.0	0	0	0
	12. Annett Inlet	Feb. 27	3 (33)	9.0	0.04	20.0	25.0
Strait open	13. Komas Bluff	Mar. 15–26	5 (10–21)	9.0	79.1 ± 20.4	99.9	87.4
	14. Qualicum	Mar. 3	7 (35)	9.0	1.3 ± 1.7	71.9	6.6
	15. Horsewell Bluff	—	8	9.0	0.1 ± 0.1	23.8	0
	16. Savary Island	Mar. 13	4 (23)	9.0	4.1 ± 4.6	86.1	1.0
	17. Atrevida Reef	—	4	9.6	0.2 ± 0.2	80.8	10.0
	18. Harwood Island	Mar. 11	4 (25)	9.0	1.1 ± 0.8	71.1	2.3
North bays	19. Hunt Inlet	Mar. 30, Apr. 10	26 (16,36)	8.5	146.3 ± 64.7	100	94.2
	20. Alliford Bay	Apr. 6	22 (17)[a]	5.5	0.01 ± 0.02	1.1	100
	21. Huston Inlet	Mar. 14–30	21 (21–30)	7.0	13.2 ± 5.6	97.2	5.0
	22. Section Cove	Mar. 26	20 (25)	7.0	9.3 ± 8.5	80.3	14.9
	23. Poole (head)	—	21	7.0	64.8	51.1	2.5
North open	24. Freeman Passage	Apr. 5, 14	26 (12,21)	8.5	1.5 ± 0.5	64.2	56.7
	25. Big Bay	Mar. 25–31	16 (16–22)	8.5	47.7 ± 5.5	99.5	63.9
	26. Cumshewa Inlet	Mar. 24	22 (29)	6.0	2.4 ± 1.2	74.4	0
	27. Alder Island	Mar. 26	20 (25)	7.0	36.6 ± 57.8	94.0	39.2
	28. Poole Inlet	Mar. 13–21	21 (16–22)	7.0	19.1 ± 31.0	100	0

[a]Not hatched.

The total numbers of predators varied by three orders of magnitude among the 28 locations (Table 2). In order to assess differences among predator populations, the sampling locations were grouped into five areas, which were (a) Barkley Sound (No. 1–4) (b) bays (No. 5–12) and (c) open shore (No. 13–18) locations in the Strait of Georgia, (d) bays (No. 19–23) and (e) open shore (No. 24-28) locations in northern British Columbia. Differences in the densities of all predator species between locations within areas were not statistically significant (Table 4). By contrast, differences among locations in pairs of areas always were significant (Table 4). The greatest differences in predator populations were seen in tests comparing Barkley Sound with other areas ($p<0.001$), with Barkley Sound locations generally having high densities of all predator types. Bay locations in both the Strait of Georgia and in northern British Columbia had greater predator densities than locations along open shorelines ($p<0.05$ and $p<0.01$, respectively). Predator densities in northern British Columbia generally were greater than in the Strait of Georgia.

The hydromedusa *Aequorea victoria* was of particular interest because it was previously recognized as a predator of fish larvae (Arai and Hay 1982; Purcell 1986, 1989). In 1984, *A. victoria* occurred over a broad geographic area, in bays and inlets of Vancouver Island, the nearby Gulf Islands, and in inlets of the Queen Charlotte Islands (Table 3). Density of this species was greatest at the head of Poole Inlet and in Kulleet Bay.

The size of the *Aequorea victoria* medusae differed greatly among locations where they were abundant. The medusae were largest in Kulleet Bay at 49 to 68 mm diameter. In Baynes Sound, they were 33 to 55 mm in diameter, and in Poole Inlet, they were 9 to 29 mm (Fig. 3). Small medusae would catch fewer larvae than large medusae.

Predation on Herring Larvae

Herring larvae were found in the guts of only eight of the 18 predator species encountered in this study (Table 5). The hydromedusa *Aequorea victoria* was the only predator seen in Baynes Sound and Kulleet Bay that had consumed herring larvae. Seventeen specimens of *Sarsia* sp., nine *Phialidium gregarium*, and one *Mitrocomella polydiademata* contained larvae in other locations. In Barkley Sound, ctenophores (*Pleurobrachia bachei*) had ingested from one to four yolksac herring larvae. This contrasts with the head of Poole Inlet, where no specimens of *P. bachei* contained the post-yolksac herring larvae present. Six specimens of the scyphomedusa *Phacellophora camschatica* contained 431 herring larvae, as well as 36 larvae of other fishes. In other locations, two specimens of the ctenophore *Bolinopsis infundibulum* and two specimens of the chaetognath *Sagitta* sp. had eaten larvae.

The numbers of herring larvae eaten daily by *Aequorea victoria* medusae at 0–5 m depth could be determined only at two stations. At one station (Fanny Bay) in Baynes Sound about 0.4% of the herring larvae were eaten by *A. victoria* in the surface 5 m on April 6 (Table 6). Three other stations were sampled in Baynes Sound, but *A. victoria* were collected in

TABLE 2. Densities of soft-bodied zooplankton predators (mean number·m^{-3} ± SD) at 28 locations in British Columbia, near the time that herring larvae hatched in 1984. The percentages of polygastric siphonophores are in parentheses.

Location		No. of species	Medusae	Ctenophores (*Pleurobrachia*)	Chaetognaths (*Sagitta*)	Siphonophores (*Muggiaea*)		Total predators
Barkley Sound	1.	7	52.7±29.5	20.2+22.0	0.3±0.6	12.1±12.3	(56)	85.3±32.8
	2.	13	160.2±108.9	25.4±29.5	24.0±14.5	7.8±12.6	(27)	217.4±127.6
	3.	12	89.0±33.4	35.2±27.4	15.7±11.1	13.8±13.9	(20)	153.6±71.6
	4.	11	40.2	2.8	0.9	3.6	(56)	47.5
Strait bays	5.	9	1.6±1.3	0,[a]	0.1±0.1	0		1.7±1.4
	6.	8	51.4±56.5	0	0.02±0.03	0.3±0.3	(38)	51.7±56.8
	7.	13	7.6±3.7	0	0.02±0.02	0.1±0.2	(60)	8.0±3.6
	8.	7	12.8	0.3	0	0		13.1
	9.	8	0.6±0.4	0,[a]	0.04±0.05	0		0.7±0.5
	10.	8	2.5±1.4	0	0.1±0.1	0		2.6±1.3
	11.	12	25.3±15.3	0.2±0.2	0.2±0.2	0.04±0.08	(0)	25.6±15.4
	12.	9	1.4	0	0.1	0.1	(20)	1.6
Strait open	13.	8	0.2±0.2	0,[a]	0.2±0.04	0		0.3±0.3
	14.	8	1.0±0.8	0.2±0.03,[a]	0	3.1±2.9	(33)	4.1±3.6
	15.	8	1.1±0.7	0	0.03±0.05	0.02±0.02	(33)	1.3±0.5
	16.	7	0.5±0.3	0.01±0.03,[a]	0.3±0.2	0		0.8±0.5
	17.	6	0.4±0.05	0.01±0.02,[a]	0.08±0.09	0		0.5±0.1
	18.	7	0.7±0.4	0.04±0.05	2.8±3.5	0		3.6±3.8
North bays	19.	15	2.2±0.9	0.1±0.1,[a]	0.3±0.2	0.5±0.8	(0)	2.6±2.3
	20.	11	66.7±22.1	0.03±0.04	2.4±0.1	1.3±0.4	(24)	70.3±22.0
	21.	11	12.3±8.8	0.8±0.8	1.8±0.7	23.2±7.2	(15)	38.1±15.7
	22.	9	13.6±2.0	0.3±0.4	7.0±5.2	2.1±0.1	(6)	23.0±7.5
	23.	11	62.2	6.0	12.0	50.8	(10)	144.1
North open	24.	11	4.0±1.3	0.02±0.05,[a]	0.3±0.1	0		4.4±1.4
	25.	11	3.1±0.7	0.2±0.1,[a]	0.5±0.6	0.1±0.2	(80)	4.0±0.2
	26.	8	7.8±1.9	0.05±0.10	1.6±1.2	0.12±0.02	(1)	9.5±2.0
	27.	13	7.4±5.0	0.3±0.4	3.4±2.6	3.7±1.8	(10)	14.8±9.6
	28.	11	6.7±9.5	0.02±0.05	1.8±2.3	7.3±9.6	(10)	18.2±19.6

[a]*Bolinopsis* present.

only three of 23 tows (total of 2573.3 m^3 filtered). No medusae were found at the surface for gut analysis, and no estimates of predation were made. At one station in Kulleet Bay, predation on herring larvae by *A. victoria* dropped from 12.5 to 3.9%·d^{-1} to zero (not detected) as larval densities decreased over 3 d (Table 6). Medusae were not found consistently for gut content analysis at the other two stations in Kulleet Bay.

Zooplankton and Microzooplankton

The densities of the zooplankton varied by two orders of magnitude among the 28 locations (Table 7). Comparisons between areas showed that the total numbers of zooplankton were statistically different in only three cases: bays in the Strait of Georgia compared with bays and with open shore in northern British Columbia (ANOVA, $p=0.01$ and $p<0.01$), and open shores compared between the Strait of Georgia and northern British Columbia ($p=0.05$). Locations in the Strait of Georgia had higher zooplankton densities than locations in northern British Columbia (ANOVA, $p=7.2\times10^{-4}$).

Copepod nauplii and copepodites were most numerous in the microzooplankton samples, and tintinnids, bivalve veligers, euphausiid and barnacle nauplii were abundant in some locations (Table 8). The densities of protozoans and copepod eggs probably were underestimated because many could pass through the 63-μm mesh of the net, and only shelled protozoans were preserved. Microzooplankton densities varied by 10-fold among the locations sampled. Comparisons between areas showed no statistically significant differences (ANOVA, $p>0.25$ in all comparisons).

Foods of Herring Larvae and Soft-Bodied Zooplankton

Prey items from the guts of first feeding herring larvae that were <10 mm in preserved SL and older larvae of 10–15 mm SL in Kulleet Bay were mostly copepod nauplii, tintinnids, and bivalve veligers (Table 9). Even though barnacle and euphausiid nauplii totalled 23% of the microzooplankton in the environment, they were not fed upon by the larvae. Few copepodites were ingested by larvae <15 mm, but they comprised 17–36% of the diets of larvae 15–25 mm of SL in 1983 (J. Grover and J. Purcell, unpubl. data).

In order to estimate if first-feeding herring larvae could obtain adequate food for survival at the sampling locations, I calculated the minimum number of prey needed to balance metabolic costs and the minimum density of prey as follows. Active first-feeding larvae respired approximately 2.6 μL O_2·mg dw^{-1}·h^{-1} at 10°C (De Silva and Tytler 1973). Daily larval respiration equals 6.6 μL O_2·$larva^{-1}$·d^{-1}, assuming 106.2 ± 9.1 μg dry weight for early post-yolksac larvae (Hay 1984). Conversion of respiration to calories using the oxycaloric equivalent of 4.9 cal·mL O_2 gives 0.033 cal·d^{-1}·$larva^{-1}$ needed to meet metabolic demands. The mean size of copepod nauplii consumed by herring larvae in Kulleet Bay was 0.20 ± 0.07 mm (J. Grover and J. Purcell, unpubl. data), equal to 0.29 μg dry weight (Durbin and Durbin 1981), and 0.002 cal·$nauplius^{-1}$ (Platt et al. 1969). The caloric demands of first-feeding larvae could be met by consuming 16.5 nauplii·d^{-1}.

Munk and Kiørboe (1985) found that herring larvae encountered prey in 4–6 L each hour at densities of 5–360 copepod nauplii·L^{-1}, and that 40% of encounters resulted in capture. Over a 14-h light period, larvae could encounter prey in 56–84

TABLE 3. Densities of hydromedusae (numbers·m^{-3}) at 28 herring spawning grounds in British Columbia in 1984. Total numbers of medusae·m^{-3} are given in Table 1. Ae = *Aequorea victoria*, Ph = *Phialidium gregarium*, Eu = *Eutonina indicans*, Mi = *Mitrocomella polydiademata*, Ob = *Obelia* sp., Sa = *Sarsia tubulosa*, Ra = *Rathkea octopunctata*, Pr = *Proboscidactyla flavicirrata*, Ag = *Aglantha digitale*.

		Leptomedusae				Anthomedusae				Limnomedusae	Trachymedusa
Location		Ae	Ph	Eu	Mi	Ob	Sa	Ra	Misc.	Pr	Ag
Barkley Sound	1.	0	17.10	0	0	2.61	23.80	1.71	0	0	7.38
	2.	1.00	30.10	1.00	1.76	103.17	3.52	4.81	0.48[a]	2.56	12.50
	3.	1.96	33.80	0.98	0	23.85	10.15	7.48	0.27[a]	0.27	19.14
	4.	0.44	8.96	0	0.44	17.53	2.57	0	2.13[d]	2.13	6.43
Strait bays	5.	0.04	0.05	0	0	0.47	0.66	0	0.02[b]	0.04	0.35
	6.	0	0.93	0	0	3.65	11.87	34.49	0	0.02	0.46
	7.	0.74	1.78	0.04	0.40	0.16	2.75	0.14	0.17[a,c]	0.21	1.22
	8.	0	0	0.76	0	1.72	1.72	4.49	3.97[b]	0	0.13
	9.	0.01	0.10	0	0	0	0.31	0	0.05	0.01	0.12
	10.	0.14	0.87	0.07	0	0.25	0.65	0.32	0	0	0.18
	11.	0	0.48	1.59	1.46	2.12	12.20	1.31	1.31[a]	0.66	4.06
	12.	0	0.53	0	0.06	0.02	0.32	0.20	0.08[b]	0	0.20
Strait open	13.	<0.001	0.05	0	0	<0.001	0.06	0	0.06[a]	0	0.02
	14.	0	0.51	0	0	0.08	0.31	0.13	0	0	0.09
	15.	0	0.16	0.02	0	0.23	0.28	0.34	0.03[b]	0	0
	16.	0	0	0	0	0	0.48	0	0.01	0.01	0.01
	17.	0	0.03	0	0	0	0.36	0	0.17[b]	0	0
	18.	0	0	0	0.01	0	0.54	0.04	0.01	0	0.10
North bays	19.	0.02	0.90	0	0.33	0.07	0.26	0.33	0.21[a,b,c]	0.05	0.02
	20	0.80	48.80	0.80	4.00	1.60	2.00	7.14	0	0	1.66
	21.	0.12	7.10	0.23	0.83	0	0.23	2.36	0.23	1.18	0
	22.	0	1.82	0	1.14	0.10	0.19	10.15	0.19[c]	0	0
	23.	6.10	51.19	0	0	0	1.24	2.15	0.68[a,d]	0.87	0
North open	24.	0	1.67	0.04	0.12	0.21	1.29	0.17	0.33[b]	0.17	0
	25.	0	1.41	0	0.55	0.10	0.25	0.88	0.13[a,b]	0	0
	26.	0	2.25	0	0.86	0	1.82	2.34	0.26[a,b]	0.90	0.17
	27.	0.07	1.06	0.07	1.06	0.07	0.33	4.10	0.40[b]	0.07	0.20
	28.	0.19	1.78	0	0	0	1.08	3.15	0.19[a,b]	0.19	0.10

[a] *Bougainvillia* sp.
[b] Family Tubularidae: *Plotocnide borealis, Hybocodon prolifer*.
[c] *Stomatoca atra*.
[d] Scyphozoan ephyrae.

TABLE 4. Differences among locations in predator populations in British Columbia. The 28 locations were grouped into five areas. No differences were seen between the predator populations among locations within each area (NS = not significant). However, differences were significant between all pairs of areas (two-way ANOVA).

		Strait of Georgia		Northern B.C.	
Location	Barkley Sound	Bays	Open shore	Bays	Open shore
Barkley	NS $p>0.5$	—	—	—	—
Strait-Bays	$p<0.001$	NS $p<0.1$	—	—	—
Strait-Open	$p<0.001$	$p<0.05$	NS, $p>0.75$	—	—
North-Bays	$p<0.05$	$p<0.01$	$p<0.005$	NS $p>0.5$	—
North-Open	$p<0.001$	$p<0.05$	$p<0.005$	$p<0.01$	NS $p<0.1$

L·d^{-1}, and meet their metabolic costs if nauplii occurred in densities of at least 0.5–0.8·L^{-1}. This estimate is lower than recent experimental estimates of 7.5 nauplii·L^{-1} (Kiøboe et al. 1985) and 12 nauplii·L^{-1} (Gamble et al. 1981). In the present study, the average microzooplankton densities varied from 37·L^{-1} in Kulleet Bay, which by all recent estimates is adequate for survival of herring larvae, to 0.8·L^{-1} in Tribune Bay, which is marginally adequate prey for the larvae.

Foods of soft-bodied zooplankters were quantified in order to determine if they could reduce the prey resources available to herring larvae (Tables 10 and 11). The diets of only three species of hydromedusae collected in this study, i.e. *Obelia* spp., *Proboscidactyla flavicirrata*, and *Aglantha digitale*, showed extensive overlap (90–100%) with the diet of larval herring (Table 10). Eight other species of soft-bodied zooplankters were shown to eat copepod nauplii. The ctenophore *Pleurobrachia bachei* examined from sampling locations No. 2 and 23 contained no prey taxa of first-feeding herring larvae, however, other data showed that ciliates and copepod nauplii, as well as copepods, were consumed by small *P. bachei* (Harris et al. 1982). Harris et al. (1982) also found ciliates, copepod nauplii, and copepods to be the prey of the chaetognath *Sagitta elegans* (Table 11). The scyphomedusa *Phacellophora camtshatica* consumed no microzooplankton prey (Table 11). The

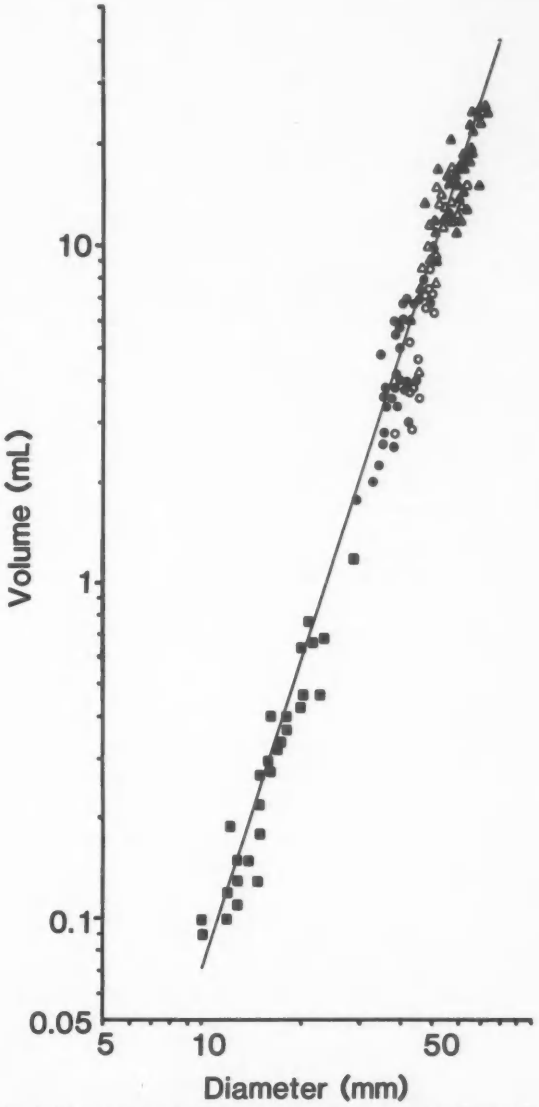

FIG. 3. Relationship of diameter to volume in preserved specimens of *Aequorea victoria* medusae. Squares = medusae from Poole Inlet, triangles = medusae from Kulleet Bay, and circles = medusae from Baynes Sound. Closed symbols are for specimens collected in 1984, and open symbols are from 1983. Regression: $y = 0.000055X^{3.09}$, $r = 0.98$, $n = 177$.

siphonophore *Muggiaea atlantica* consumed copepod nauplii and small copepods ≤0.9 mm in cepholothorax length, which could be foods of herring larvae (Table 11). Nine hydromedusa species, scyphomedusae, siphonophores, ctenophores, and chaetognaths consumed copepods, and therefore could affect the production of copepod nauplii.

The numbers of zooplankton prey consumed by soft-bodied predators that are also foods of herring larvae (i.e. tintinnids, bivalve veligers, copepod nauplii, and copepodites) were calculated from the numbers of these prey eaten by each predator species (Tables 10 and 11) multiplied by the densities of each species in situ (Tables 2 and 3). Consumption of these prey by soft-bodied predators varied from 1.3 to 355.7 prey·m^{-3}·d^{-1}, or 0.02 to 11.86% of the prey standing stock (Table 12). In 17 of 21 locations, consumption of microzooplankton was estimated at less than 1% of the standing stock.

The ratio of the numbers of microzooplankton foods in the environment to the number of predators is used here as an index of the relative likelihood for survival of herring larvae in the sampling locations (Table 12). These ratios varied over three orders of magnitude, suggesting that the larvae in different environments may encounter very different conditions for survival and growth. The highest ratios, indicating relatively favorable conditions, occurred at locations in the Strait of Georgia. These ratios were significantly different from the ratios in northern British Columbia where generally food densities were low and predator densities high (ANOVA, $p = 0.05$). The ratios in Barkley Sound were ≤0.05, except at No. 4 (0.6). Extremely high predator abundances in three locations in Barkley Sound (61.4–98.3·m^{-3}) and low food densities (≤5·L^{-1}) suggest difficult conditions for larval survival.

Discussion

Predation on Herring Larvae

Most of the soft-bodied predators of herring larvae found in the present study had been found earlier to eat fish larvae. These predators of fish larvae include *Aequorea victoria*, *Sarsia tubulosa*, and *Phialidium gregarium* (tested by Arai and Hay 1982), *Mitrocomella polydiademata* (Purcell 1989), *Phacellophora camtschatica* (Larson 1978), *Sagitta* spp. (reviewed in Alvariño 1985), and *Pleurobrachia bachei* (Stevenson 1962; van der Veer 1985; Frank 1986). Species that had been identified as larval predators elsewhere, but which did not contain herring larvae in the present samples included *Bougainvillia multitentaculata*, *Eutonina indicans* (laboratory tests, Arai and Hay 1982), and *Rathkea octopunctata* (net-collected specimens, Lebour 1922, 1923; laboratory tests, Sveshnikov 1963). My conclusions support those of Arai and Hay (1982) which showed that *Obelia* spp. and *Proboscidactyla flavicirrata* did not eat herring larvae.

Specimens in eight of the 18 species of soft-bodied predators contained herring larvae. However, many larvae were found in gut contents only of *Aequorea victoria* and *Phacellophora camtschatica*, and of predators in Barkley Sound where sampling coincided with larval hatching. Newly-hatched larvae are most vulnerable to predation (Bailey and Batty 1984; Purcell et al. 1987), and they were caught in Barkley Sound by *Phialidium gregarium*, *Sarsia tubulosa*, *Pleurobrachia bachei*, and *Sagitta* sp. In contrast, *P. bachei* of the same or greater size at the head of Poole Inlet did not capture post-yolksac herring larvae. For the soft-bodied predators other than *A. victoria* and *P. camtschatica*, capture of herring may be restricted mainly to early-yolksac larvae.

Synchronous hatching of demersal herring eggs results in high larval densities that may satiate the feeding capabilities of most soft-bodied predators (Bailey and Houde 1989). Because of the small gut capacity of most hydromedusae, ctenophores, and chaetognaths, individual predators could not consume large numbers of larvae, even when larval densities were high. Therefore, satiation of soft-bodied predators (other than large scyphomedusae and hydromedusae like *Aequorea victoria*) may limit predation at hatching.

TABLE 5. Observations of predation on fish larvae by soft-bodied zooplankton at herring spawning grounds in British Columbia in 1984. All species were examined at all 28 locations. NQ = not quantified.

Location		Number examined	Herring eaten·predator^{-1}	Other larvae·predator^{-1}	Fish larvae (% of all prey)
Barkley Sound	1. Forbes Island				
	Pleurobrachia	114	0.08	0	17.0
	Sarsia	38	0.45	0	NQ
	2. Prideaux Island				
	Pleurobrachia	281	0.03	0	19.6
	Sagitta	106	1 obs.	0	20.0
	3. Nettle Island				
	Pleurobrachia	168	0.10	0	24.6
	Phialidium	109	1 obs.	0	NQ
Strait bays	5. Baynes Sound				
	Aequorea[a]	79	0.23	0.04	NQ
	7. Kulleet Bay				
	Aequorea[a]	72	0.28	0.07	0.5
North bays	19. Hunt Point				
	Bolinopsis	NQ	1 obs.	0	NQ
	Mitrocomella	NQ	5 in 1 medusa	0	NQ
	Phialidium	44	0.04	0	NQ
	21. Huston Inlet				
	Phialidium	396	0.03	0	NQ
	23. Poole (head)				
	Aequorea[a]	1	2.0	1.0	8.6
	Phacellophora[a]	6	71.8	2.8 gadid 3.2 misc.	27.3
	Phialidium	188	0	0.01	NQ
	Pleurobrachia	147	0	0	0
North open	25. Big Bay				
	Bolinopsis	NQ	1 obs.	0	NQ
	27. Alder Island				
	Sagitta	123	1 obs.	0	NQ

[a]Individually collected.

TABLE 6. Predation rates of *Aequorea victoria* medusae on herring larvae in Fanny Bay in Baynes Sound and Kulleet Bay at 0–5 m depth. Numbers of medusae examined are in parentheses. T = time interval (14 h day, 10 h night, 24 h total).

Location		Larvae in each medusa	Larvae·medusa·T^{-1}	Medusae ·m^{-3}	Larvae eaten·m^{-3}·T^{-1}	Larvae ·m^{-3}	% of Larvae eaten·T^{-1}
Fanny Bay							
day	14 h	0.06 (35)	0.2	0.4	0.08	62.5	0.13
night	10 h	0.36 (44)	1.0	0.1	0.10	43.1	0.23
total	24 h						0.36
Kulleet Bay							
April 9	24 h	2.0 (12)	13.7	0.35	4.8	38.5	12.5
April 10	24 h	0.2 (10)	1.4	0.14	0.2	5.1	3.9
April 11	24 h	0 (21)	0	0.23	0	0.7	0

TABLE 7. Densities of zooplankton (numbers·m^{-3}) at 28 herring spawning grounds in British Columbia in 1984.

	Copepods	Total
Barkley (No. 1–3)	558.5 ± 247.7	1 764.5 ± 843.1
(No. 4)	6 863.9	15 059.2
Strait-bays	2 187.1 ± 1 601.5	5 630.0 ± 3 322.32
Strait-open	2 921.8 ± 2 248.3	3 658.1 ± 2 713.5
North-bays	867.6 ± 488.0	1 192.2 ± 716.4
North-open	649.6 ± 560.6	884.3 ± 560.8

In contrast, specimens of the large hydromedusa *Aequorea victoria* and the scyphomedusa *Phacellophora camtschatica* can contain dozens of larvae, and can eat at least 90 larvae·medusa^{-1}·d^{-1} (Purcell 1989, herein). *Aequorea victoria* occurred at nine of the 28 locations, and its predation effect on herring larvae was estimated to be 0.4%·d^{-1} and 0–12.5%·d^{-1} at two locations. *Phacellophora camtschatica* was found at only one location. Both *A. victoria* and *P. camtschatica* consumed post-yolksac herring larvae (Purcell et al. 1987; Purcell 1989). Because of its wide distribution, occasional occurrence at high densities (>0.5·m^{-3}), its ability to eat many larvae and post-yolksac larvae, *A. victoria* was the key soft-bodied predator of herring larvae at sampling locations in British Columbia in 1984.

The predation effects of soft-bodied predators other than *Aequorea victoria* could not be calculated because of the generally low incidence of larvae in the predators' guts, and

TABLE 8. Densities of microzooplankton (numbers·L^{-1}) at 21 herring spawning grounds in British Columbia.

Location		Tintinnids	Bivalve veligers	Copepod nauplii	Copepodites	Invertebrate eggs	Misc.[a]	Total
Barkley Sound	1.	0.12	0.15	0.98	0.43	0.20	1.12	3.0
	2.	0.07	0.71	1.90	1.39	0.07	4.86	9.0
	3.	0.18	0.51	1.96	1.09	1.28	1.88	6.9
	4.	0.07	0.82	4.77	3.95	0	5.59	15.2
Strait bays	5.	0.05	0.01	0.48	5.55	2.66	1.64	10.4
	6.	0.07	0.07	10.05	3.87	0	3.74	17.8
	7.	3.65	0.23	23.52	5.71	3.65	10.96	47.7
	9.	0.15	0	0.23	0.40	0.04	0.82	1.6
Strait open	13.	0	0	3.12	1.43	0.58	1.12	6.2
	14.	0.07	0	3.39	2.43	0	1.71	8.2
	16.	0	0	9.51	22.27	0	12.22	44.0
	17.	0	0	2.99	2.34	0	1.56	6.9
North bays	19.	0	0	7.58	2.30	0.07	1.35	11.3
	20.	0	2.25	7.43	2.18	1.84	1.70	15.4
	21.	0.05	0	1.93	1.12	0.71	1.83	5.6
	22.	0	0	1.15	0.03	0.19	0.63	2.0
	23.	0.07	0.03	3.62	1.61	0.38	2.19	7.9
North open	24.	0.34	0	2.97	1.13	0.24	2.02	6.7
	25.	0.31	0.05	15.50	1.28	0.46	6.08	23.7
	27.	0	0.10	1.69	0.41	0.41	0.80	2.4
	28.	0.24	0	1.01	0.37	0.69	1.50	3.8

[a]Barnacle and euphausiid nauplii.

TABLE 9. Microzooplankton in the environment and consumed by herring larvae in Kulleet Bay.

	Tintinnids	Bivalve veligers	Copepod nauplii	Copepodites	Copepod eggs	Misc.[a]	Notes
Environment (%)	7.7	0.5	49.5	12.0	7.7	23.1	47.7·L^{-1} 2 samples
Consumed (%)[b]							
<10 mm SL	6.8	3.4	84.4	1.2	4.2	0	263 prey 69 larvae
10–15 mm SL	0.9	6.4	90.4	0.9	1.4	0	220 prey 48 larvae

[a]Barnacle and euphausiid nauplii.
[b]J. Grover and J. Purcell (unpubl. data).

lack of digestion rate data. The numbers of larvae found in the predators may have been reduced due to gut evacuation during collection in the plankton net (Purcell 1989). Predation may have been missed in some locations where sampling followed hatching by several days, thereby resulting in high percentages of post-yolksac larvae, which few species of soft-bodied zooplankton caught.

In this study, soft-bodied predators were most abundant in bays and inlets. Zavodnik (1987) showed how wind, currents, and geomorphological features concentrate scyphomedusae in shallow coastal waters. Herring spawn in protected waters of the British Columbia coast, often in bays or inlets (Figs. 1 and 2), and the larvae may hatch in areas of greatest predator abundance.

Predation on Microzooplankton

Consumption of copepods and microzooplankton was estimated for all of the soft-bodied predator species. These figures are believed to be minimum estimates for the following reasons: (1) Digestion times for copepods were assumed to apply to microzooplankton, because no rates were available, however small prey may require less digestion time (Purcell 1982), (2) Gut evacuation appeared to be frequent in several hydromedusa species because of the low incidence of prey in the guts (i.e. Phialidium gregarium, Obelia spp., *Aglantha digitale* (Table 10)). Thus, prey consumption in locations where those species were abundant may be underestimated. (3) No data were available for prey consumption rates of siphonophore eudoxids, therefore they were not included in the calculations. Their densities were greater than the polygastric colonies in 15 of 19 locations where siphonophores were collected. (4) No densities or dietary information were available for the lobate ctenophore *Bolinopsis infundibulum*. This species was present at nine of the 28 locations.

Soft-bodied zooplankton was estimated to consume <1%·d^{-1} of the standing stocks of copepods and microzooplankton in 17 of the 28 locations. Only in Barkley Sound did consumption of those prey exceed 1%·d^{-1} (1.8 to 11.9%·d^{-1}). Population production rates of those prey would be greater than the consumption estimates. For example, Durbin and Durbin (1981) estimated production of the copepod *Acartia hudsonica* at 7.0–7.3°C to be 15–18%·d^{-1}. Tintinnid population growth can exceed 50%·d^{-1} at temperatures <10°C (Verity 1985). Therefore, grazing of microzooplankton prey by soft-bodied predators removed only a small fraction of the daily production,

TABLE 10. Percentages of microzooplankton and other prey found in the diets of hydromedusa species common at herring spawning grounds in British Columbia. Prey items important to herring larvae are in the first four columns. The numbers of those prey eaten·d^{-1}·medusa^{-1} are estimated by use of the numbers of prey·medusa^{-1} and digestion data from Larson (1987).

Hydromedusae	Tintinnids (%)	Bivalve veligers (%)	Copepod nauplii (%)	Copepods (%)	Euph. eggs (%)	Barnacle nauplii (%)	Larvaceans (%)	Fish eggs and larvae (%)	Prey/ medusae	Prey eaten·d^{-1} ·medusa^{-1}
Leptomedusae										
Aequorea[a,d]	[c]	0	[c]	2.0	[c]	11.7	34.5	48.6	1106/24	4.1
Phialidium[b,d]	0,[f]	0,[f]	0	1.8	54.6	0,[f]	36.4	5.4	55/24	0.25
Eutonina[b,d]	0	0	1.4	1.4	89.5	2.1	3.2	0.1	630/28	3.8
Mitrocomella[b,d]	0,[f]	0,[f]	0	2.3	0	2.3	95.4	[c,a]	44/18	0.7
Obelia[a,e]	3 obs.	0	0	0	0	0	0	0	3/523	0.03
Anthomedusae										
Sarsia[b,c]	0,[f]	0,[f]	2.5	13.0	0,[f]	83.9	0,[f]	0.3	360/26	12.9
Rathkea[a,e]	0	0	0	0	0	62.5	25.0	1 ? obs.	8/601	0
Bougainvillia[b,d]	0	0	2.4	1.2	0.6	94.0	1.2	0	168/15	2.4
Hybocodon[b,d]	5.3	0	5.3	68.4	0	21.0	0	0	19/12	7.0
Limnomedusae										
Proboscidactyla[a,e]	69.3	27.7	1.0	0,[f]	1.0	1.0	0,[f]	0	101/53	11.3
Trachymedusae										
Aglantha[a,e]	60.0	0,[f]	10.0	10.0	20.0	0,[f]	0,[f]	0	40/391	0.6

[a]Data from herring spawning areas in late March–early April 1983–86.
[b]Data from Friday Harbor Washington, March 11–21, 1982.
[c]Present in small numbers.
[d]Collected individually.
[e]From plankton net tow samples. Prey eated·d^{-1} is probably low due to gut evacuation.
[f]≤ 2% of gut contents (Larson 1985).

TABLE 11. Percentages of microzooplankton, zooplankton, and fish larvae in the diets of ctenophores, chaetognaths, scyphomedusae, and siphonophores at sampling locations in British Columbia and in nearby waters. Prey items important to herring larvae are in the first three columns. The numbers of those prey eated·d^{-1}·predator^{-1} are estimated by use of the number of prey·predator^{-1} and digestion data from Larson (1987) for *Pleurobrachia*, and by assuming 5 h digestion for *Phacellophora*.

	Ciliates (%)	Copepod nauplii (%)	Copepods (%)	Clado-cerans (%)	Larva-ceans (%)	Mero-plankton (%)	Gelatinous zooplankton (%)	Fish larvae (%)	Prey/ predators	Prey eaten·d^{-1}· predator^{-1}
Pleurobrachia										
2. Prideau	0	0	2.4	48.7	1.2	16.7	0	31.0	84/114	0.1
23. Poole head	0	0	13.1	0	0.5	86.4	0	0	213/20	9.6
Saanich Inlet	16.1	9.3	71.4	0	0	3.2	0	0	378/?	—
Sagitta										
Saanich Inlet[b]	3.2	14.3	82.5	0	0	0	0	0	372/?	2[d]
Phacellophora										
23. Poole head[a]	0	0	6.9	0	27.2	15.2	23.5	27.3	1717/6	94.8
Muggiaea										
Friday Harbor[a,c]	0	27.6	72.4	0	0	0	0	0	141/117	5.5–10.5[c]

[a]Collected individually.
[b]Harris et al. (1982).
[c]Polygastric colonies, Purcell (1982).
[d]Purcell and Kremer (1983).

and the predators probably did not reduce microzooplankton available to herring larvae for food.

Low prey densities present several problems for herring larvae. Increased swimming to find enough prey increases metabolic demands, which must be met with additional prey items. Increased activity also would result in greater encounter with predators. Slow growth rates at low prey densities would lengthen the period of time that larvae are vulnerable to predators. Therefore, survival of larvae must decrease as prey densities decrease.

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TABLE 12. Densities of soft-bodied predators shown to eat herring larvae (data from Tables 2 and 5), the quantities of microzooplankton foods eaten by soft-bodied predators (calculated from data in Tables 2, 3, 8, 9, 10 and 11), and the ratios of microzooplankton foods of larvae to the numbers of predators. The percentages of microzooplankton eaten of densities in the environment are in parentheses.

Location		Soft-bodied predators of larvae ($No.\cdot m^{-3}$)	Fish larva foods eaten by soft-bodied predators ($No.\cdot m^{-3}\cdot d^{-1}$)	Larval foods$\cdot L^{-1}$ / predators$\cdot m^{-3}$
Barkley Sound	1.	61.42	355.7 (11.86)	0.03
	2.	86.96	164.8 (1.83)	0.05
	3.	98.30	217.1 (3.15)	0.04
	4.	16.15	79.1 (0.52)	0.6
Strait bays	5.	0.85	9.7 (0.09)	10.3
	6.	12.92	154.6 (0.87)	1.1
	7.	5.92	43.6 (0.09)	6.2
	9.	0.46	4.3 (0.27)	1.7
Strait open	13.	0.13	1.3 (0.02)	39.1
	14.	0.82	9.8 (0.12)	7.7
	16.	0.79	6.9 (0.02)	40.2
	18.	3.38	12.6 (0.18)	1.3
North bays	19.	1.92	5.6 (0.05)	5.2
	20.	59.05	54.6 (0.35)	0.2
	21.	11.05	43.4 (0.75)	0.3
	22.	10.35	18.4 (0.92)	0.1
	23.	76.37	169.3 (2.14)	0.08
North open	24.	3.43	22.1 (0.33)	1.4
	25.	2.92	5.7 (0.02)	6.0
	27.	6.22	19.4 (0.79)	0.3
	28.	4.73	22.3 (0.59)	0.5

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A Partial Bias Correction Factor for Stock–Recruitment Parameter Estimation in the Presence of Autocorrelated Environmental Effects

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Stock–recruitment time series often give a distorted picture of average recruitment rates, with high productivities per spawner being overrepresented at low stock sizes. This distortion is exaggerated by autocorrelation among years in environmental effects on productivity. The common procedure of fitting a stock–recruit curve and then analysing residuals from the curve will result in a substantial underestimate of the autocorrelation among environmental effects. Previous studies have recommended using Monte Carlo simulations to estimate the bias in stock–recruit model parameter estimates. These simulations can generally be avoided by using a simple correction equation. However, deviations from the corrected stock–recruit curve will not give better estimates of autocorrelation patterns in environmental effects, and hence will not help to provide better forecasts and stronger tests for factors that may be causing the effects.

Les séries chronologiques de recrutement des stocks donnent souvent un aperçu faussé des taux moyens de recrutement; ainsi, la productivité élevée par géniteur se trouve à être sur-représentée dans les stocks peu importants. Cette distorsion se trouve exagérée par une autocorrélation d'une année à l'autre des effets écologiques sur la productivité. La méthode courante d'ajuster une courbe de stock-recrue et ensuite d'analyser la variance résiduelle de la courbe conduit à une sous-estimation importante de l'autocorrélation entre différents effets écologiques. Au cours d'études antérieures, certains chercheurs ont recommandé d'utiliser la méthode de Monte Carlo pour évaluer l'erreur systématique associée aux évaluations des paramètres appliqués aux modèles de stock-recrue. On peut généralement éviter d'utiliser ces simulations en appliquant une équation simple de correction. Cependant, les écarts par rapport à la courbe corrigée de stock-recrue n'améliorent pas les évaluations des patterns d'autocorrélation des effets écologiques; ainsi, cela n'aide pas à obtenir de meilleurs prévisions et des tests plus efficaces des facteurs qui peuvent être à l'origine des effets observés.

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The detection of recruitment overfishing is a central problem in fisheries management. Detection is complicated in most stocks by extreme recruitment variation due to factors other than spawning stock size, and by the nonrepresentative sampling of stock–recruitment observations that occurs when environmental effects are allowed to influence stock sizes over time (Walters 1985). The problem of nonrepresentative sampling can be likened to the results that would be obtained by a naive experimenter who sets out to measure average recruitment rate at a series of contrasting spawning stock sizes, but chooses his test spawning stock levels by moving the level up whenever he sees an above-average result and moving it down whenever he sees a below-average result. The consequence of such nonrepresentative sampling is that recruitment rates will be on average too high at low stock sizes, and too low at high stock sizes. When the deviations from average are strongly correlated over time, recruitment rate may even appear to decline with increasing stock size (i.e. a dome shaped stock–recruit curve) when in fact the average long term relationship is independent of stock size or increasing with stock size (Armstrong and Shelton 1988; Walters and Collie 1988). By fitting a recruitment curve through a nonrepresentative collection of sample points, one obtains a set of residuals that are far too small and have a weaker autocorrelation structure than was in fact present; that is, both the magnitude and temporal structure of environmental effects will be underestimated, and forecasts will fail accordingly.

For most fisheries it is not practical to overcome the naive experimenter's design problem by deliberately holding spawning stock size at a set of carefully controlled levels for long enough to obtain a representative sample of recruitment rates at each level. Instead it is necessary to develop statistical models that attempt to estimate and remove the bias due to nonrepresentative sampling. Previous authors have recommended using Monte Carlo simulations to estimate bias (Caputi 1988; Goodyear and Christensen 1984; Kope 1988; Walters 1985; Walters and Staley 1987). This paper derives an analytical bias correction term for least squares estimates of parameters for the Ricker stock–recruit equation. Use of the correction in analyses of recruitment time series will result in more conservative estimates of optimum harvest rates, and higher estimates of the optimum spawning stock size.

Derivation of the Bias Correction

This section derives the bias correction in two steps. First, standard least squares estimators are presented, and an analytical expression for the bias is derived. This expression cannot

be used directly as a bias correction, since it involves the unknown parameter values. The second step is then to find an approximation to the bias expression, using a crude assumption about population constancy (balance of production and harvest rates) to eliminate dependence of the correction term on the parameters.

Assume that the Ricker model is written in the form

$$(1)\quad R(t) = S(t-k)\exp\{a + bS(t-k) + w(t)\}$$

where $R(t)$ = recruits in year t, $S(t-k)$ = spawners k years earlier (k = cycle length, age at recruitment), $\exp\{a\}$ = maximum recruits per spawner, b = density dependence parameter (generally negative), and $w(t)$ is an autocorrelated environmental effect with total variance σ^2. Assume that $w(t)$ can be written as

$$(2)\quad w(t) = rw(t-1) + v(t)$$

where r = lag 1 autocorrelation and $v(t)$ = independent normal deviate with variance σ_v^2 (implying $\sigma^2 = \sigma_v^2/(1-r^2)$). In my experience with many stock–recruit data sets, I suspect that r is generally between 0.2 and 0.6, indicating strong interannual persistence of environmental effects; however, I cannot test this suspicion due to the bias problems discussed below.

Standard least squares estimators for a, b, and r are given by a two stage procedure (Anderson and Wilen 1985). Letting $y(t) = \log(R(t)/S(t-k))$, first estimate b and a by linear regression of y(t) on $S(t-k)$:

$$(3)\quad b^* = \Sigma(y(t)-\bar{y})(S(t-k)-\bar{s})/\mathrm{SSX}$$

$$(4)\quad a^* = \bar{y} - (b^*)(\bar{s})$$

where $\mathrm{SSX} = \Sigma(S(t-k)-\bar{s})^2$ and the sums are over the n observation pairs $S(t-k)$, $y(t)$ available. Next compute an estimate r^* from the residuals $\hat{w}(t)$ from this regression, as

$$(5)\quad r^* = K\Sigma\hat{w}(t)\hat{w}(t+1)/\Sigma\hat{w}^2(t)$$

where the sums are over $t = 1$ to $n-1$ and K is the Hurwicz first-order bias correction $K = (n^2-1)/(n^2-2n+3)$ derived by Nahorski and Studzinski (1985). Next, use this estimate of r to form the corrected regression variates $y'(t) = y(t) - r^*2y(t-1)$ and $x'(t) = S(t-k) - r^*S(t-k-1)$. As the second stage, regress y' and x' to obtain b'^* and a'^*. These estimates will be more efficient (lower variance) than b^* and a^*, but will be just as biassed due to nonrepresentative sampling effects.

The bias from nonrepresentative sampling is most easily seen by substituting $y + b(S(t-k)-\bar{s}) + w(t) - \bar{w}$, the assumed value of $y(t)$ under the model (where $\bar{w}$ is the realized mean of $w(t)$ in the sample series), into the estimation equation (3) for b^*. After some rearranging of terms, this results in

$$(6)\quad b^* = b + [\Sigma(S(t-k)w(t) - n\bar{w}\bar{s}]/SSX$$

where again n is the number of regression sample points. If the spawning stocks were chosen by a careful experimenter to be independent of the environmental effects $w(t)$, then the expected value of the expression in brackets would be zero and b^* would be unbiassed. Often the term $\Sigma S(t-k)w(t)$ can be ignored, since it represents covariation between spawning stocks affected by $w(t-k)$, $w(t-k-1)$, etc. and $w(t)$. The key cause of bias is the term $n\bar{w}\bar{s}$, which represents covariation between $w(t)$ and all subsequent $S(t)$, i.e. nonrepresentative sampling of $S(t)$ values. For most cases, the bias will be essentially equal to the expected value of $-n\bar{w}\bar{s}/\mathrm{SSX}$, so that the absolute value of b^* will be too large (the regression estimate b^* is generally negative in the first place) and a^* will be correspondingly overestimated.

The key problem in finding a bias correction is to estimate the expected value of $\bar{w}\bar{s} = (\Sigma w)(\Sigma S)/n^2$. Notice that this product of sums contains every possible product of $w(i)$ times $S(j)$ that have occurred in the regression series. To find the expected value of such products, the $S(j)$ terms must be expressed in terms of the past $w(t)$ values that affected them, so that expected values of the $w(i)w(t)$ covariance effects can be estimated (expected value of $w(i)w(t) = \sigma^2 r^{|i-t|}$). If each line of the population time series is roughly constant ($S(t+k)$ on average equal to $S(t)$), then the Ricker model can be written very approximately as

$$(7)\quad S(t) \approx S(t-k)\,(1 + w(t))$$

This equation is based on two approximations: (1) $\exp\{w\} \approx 1 + w$ for the most probable w values, and (2) $\exp\{a + bS(t-k)\}(1 - h(t)) \approx 1.0$ where $h(t)$ is the exploitation rate in year t. Approximation (2) says essentially that harvesting takes all of the surplus $R(t) - S(t)$ in typical years, and that the density dependent effect $bS(t-k)$ does not vary enough to substantially affect variability in $S(t)$ compared with the impacts of $w(t)$. Substituting the approximation equation (7) for each S into (Σw) (ΣS) and ignoring terms larger than r^2 (autocorrelation effects at lags greater than 2), much tedious algebra reveals that the expected value of (Σw) (ΣS) is given approximately by

$$(8)\quad E\{(\Sigma w)(\Sigma S)\} \approx k(\bar{s})\sigma^2(1 + 2r)m(m-1)/2$$

where $m = n/k$ is the number of recruitment "cycles" in the regression data set. For stocks with sharp cyclic variation of period k years (such as Fraser River sockeye salmon with $k = 4$), the term $k(\bar{s})$ can be replaced by $\bar{s}(1) + \bar{s}(2) + \ldots + \bar{s}(k)$ where $\bar{s}(i)$ is the mean spawning stock in cycle line i. The term $2r$ represents covariations between $w(t)$ and both $w(t-1)$ and $w(t+1)$. The term $m(m-1)/2 = (m-1) + (m-2) + \ldots + 1$ represents the number of times that $w(1)$, $w(2)$, etc. occur in the wS products.

The final bias correction formula is given by substituting equation (8) into equation (6), to give the corrected estimate b^{**} as

$$(9)\quad b^{**} = b^* + \sigma^2(\bar{s})(0.5 + r)[(n/k) - 1]/\mathrm{SSX}$$

To correct for bias in b^*, add the term σ^2. . . to it (which will generally make it less negative). To correct for bias in a^*, apply the bias correction to b^* before calculating a^* from equation (3). Notice that the correction is very sensitive to r (proportional to r), so a key requirement is to use a reasonable estimate of r. As noted earlier, r^* from the ordinary regression residuals is generally biassed downward. One simple strategy is to initially assume $r = 2r^*$, then reestimate r from the corrected residuals $y(t) - a^{**} - b^{**}S(t-k)$ and redo the bias correction; in Monte carlo experiments, I have found that this strategy results in r estimates that are still somewhat low (10–20%).

Monte Carlo Tests

Equation (9) is not an exact bias correction. To see how well it might work in practice, I generated fake data sets with known parameter values and applied the correction procedure to these sets.

For all sets, I used the true values $a = 1.0$, $b = 1.0$, $\sigma^2 = 0.8$, $n = 20$, and $k = 4$. These values correspond to a relatively unproductive and variable salmon stock with a 4-yr life cycle

TABLE 1. Uncorrected and corrected least squares estimates of the Ricker a,b parameters and the lag 1 environmental autocorrelation parameter r. Estimates are means of 1000 monte carlo trials with $a=1$, $b=1$, r values as tabled, variance of random effects $\sigma^2=0.8$, and 20 years data for a fish with fixed 4-yr life cycle. Initial escapement cases (cyclic, smooth, overfished) described in text. Using 1000 trials, standard errors of the means presented below are in the order of 1–2% of the mean values.

	Uncorrected estimates			Corrected estimates		
	a	$-b$	r	a	$-b$	r
Cyclic						
$r=0.0$	1.04	1.75	−0.05	1.04	1.54	0.04
$r=0.2$	1.04	1.92	0.12	1.01	1.42	0.13
$r=0.4$	1.02	1.86	0.30	0.99	1.42	0.31
$r=0.6$	1.03	2.00	0.45	0.98	1.14	0.48
Smooth						
$r=0.0$	1.08	1.17	−0.06	1.00	1.06	0.07
$r=0.2$	1.08	1.22	0.10	0.96	0.95	0.12
$r=0.4$	1.12	1.35	0.26	0.94	0.93	0.29
$r=0.6$	1.12	1.51	0.42	0.87	0.83	0.46
Overfished						
$r=0.0$	1.10	2.06	−0.07	1.06	1.59	0.07
$r=0.2$	1.14	2.17	0.10	1.00	1.25	0.12
$r=0.4$	1.16	2.75	0.27	0.99	1.15	0.30
$r=0.6$	1.15	3.60	0.42	0.93	1.14	0.4

and 20 years data available. For all sets, I assumed a constant fishing rate for each of the four cycle lines, with the rate set differently among lines so as to maintain (on average) any differences in the initial relative abundances of the lines (see Walters and Staley 1987). Three initial abundance patterns were tested (see Kope 1988 for a discussion of the importance of initial conditions to the bias estimates): (1) a "cyclic dominance" pattern where $S(-3)=.4, S(-2)=.04, S(-1)=.004$, and $S(0)=.0004$; (2) an "even run" pattern with $S(-3)=S(-2)=S(-1)=S(0)=.4$; and (3) a "severe overfishing" pattern with $S(-3)=S(-2)=S(-1)=S(0)=0.1$ (i.e. stock at 10% of its unfished equilibrium size). I generated environmental variations with autocorrelations ranging from 0.0 to 0.6. I ran 1000 Monte Carlo trials to test each pattern of initial abundance and environmental correlation.

As shown in Table 1, equation (9) performs well in correcting for bias in a and b in the "even run" situation, giving close to true average estimates for a and conservatively low estimates for b when r is large. This means that using the bias correction will on average result in correct estimates of the optimum exploitation rate, but overestimates of the optimum escapement level. However, the environmental correlation is underestimated, so it remains wise to use $2r^*$ as the assumed r in equation (9). I could find no way to correct for this bias.

The situation is not so good for the cyclic dominance case. Here the bias in a is small in the first place, though the correction essentially eliminates it. However, the bias in b is very large, even after the correction is applied. This means that the optimum escapement will be underestimated, as noted in Walters and Staley (1987). Again the environmental correlation is underestimated, and even providing equation (9) with the correct r does not substantially reduce the bias in b. With 20 years data, there is only one cycle line that gives information at all about b (five observations from the $S(-3)$ line), and with so few observations the approximations in equation (9) are obviously not valid.

Results for the severe overfishing case are also somewhat discouraging. As for the cyclic escapement case, the a parameter estimates are quite close even without correction, and the b parameter is grossly overestimated without correction. The correction helps considerably for b, especially for high r, but there is still a serious risk of grossly underestimating the optimum spawning stock (concluding that the optimum is near the historical average of 0.1 when in fact it is near 0.5).

Discussion

While the bias correction equation (9) provides insight about the relative importance of environmental variation and correlation in causing bias in stock–recruit parameter estimates, its performance is disappointing in two respects. First, it is not completely successful in extracting information about the b parameter for cases where all the data have been gathered under conditions of severe recruitment overfishing (mean spawning stock much lower than the unfished equilibrium a/b). When the data contain practically no information about b, both the uncorrected and corrected regressions tend to produce b estimates implying that the optimum spawning stock is near the historical average. However, basing target escapement policy on the corrected estimator of b would at least result in a tendency to "probe" toward higher escapements, leading eventually to better information about the actual optimum.

Second, the bias correction does not result in substantially better estimates of the environmental autocorrelation parameter r. This means that it will be of limited utility in helping to reconstruct historical patterns of environmental effects, and in developing forecasts of recruitment based on assuming $w(t)=rw(t-1)$. It appears that unless the mean stock recruit relation (parameters of stock–recruit equation) are known in advance, attempts to remove the component of recruitment variation due to spawning stock size are likely to result in underestimates of the autocorrelation in environmental effects.

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Aggregations of Berried Lobsters (*Homarus americanus*) in Shallow Waters off Grand Manan, Eastern Canada

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The relative abundance, size, and sex frequencies of trap-caught lobsters were determined from five areas near the northern end of Grand Manan during August–September 1982 and August 1983. Large numbers of berried (ovigerous) females (90/100 trap hauls) and few male or nonberried female lobsters were caught in shallow (1–22 m) depths close to the shoreline in one area. The sex ratio was near 50% males in deeper areas. In the shallow area, SCUBA divers observed mature lobsters excavating bowl-shaped depressions in the sand-clay substrate and confirmed the high density of berried females indicated by the trap catches. Berried females may seek and congregate in areas favourable for egg development and larval dispersal. During summer, shallow areas provide warmer water than deeper areas and therefore allow faster egg development and egg extrusion. Also, the shallow waters with strong tidal currents would allow rapid dispersal of newly hatched larvae.

L'abondance relative et la fréquence par taille et par sexe des homards pris dans des cages ont été déterminées chez des sujets capturés dans cinq secteurs près de l'extrémité nord de Grand Manan en août–septembre 1982 et en août 1983. Des femelles ovigères en grand nombre (90 remontées de cages sur 100) et peu de mâles ou de femelles non ovigères ont été capturés en eaux peu profondes (1–22 m) à proximité du rivage dans un secteur. En profondeur, il y avait 50 % de mâles. Dans les secteurs peu profonds, des plongeurs en scaphandre autonome ont observé des homards parvenus à maturité qui creusaient des cavités en forme de cuvette dans le substrat de sable et d'argile; ils ont confirmé la présence de femelles ovigères en concentration élevée. Ces femelles peuvent rechercher les secteurs propices au développement des oeufs et à la dispersion des larves, et s'y réunir. Durant l'été, l'eau des hauts-fonds est plus chaude que l'eau profonde : le développement des oeufs et l'extrusion se trouvent donc accélérés. En outre, les eaux peu profondes sont agitées par de forts courants de marée, ce qui favorise la dispersion des larves nouvellement écloses.

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Determining the distribution and abundance of brood stock is an important requisite for understanding the source and level of recruitment of larvae into a population. Estimation of brood stock abundance in lobsters, *Homarus americanus*, has been hampered by ignorance of the exact seasonal location and migratory behaviour of berried (ovigerous) females. Recently, concentrations of berried females were found in the Bay of Fundy and off southwestern Nova Scotia (Campbell and Pezzack 1986). Also, tagged mature female lobsters make seasonal deep-shallow migrations in coastal waters of these areas (Campbell and Stasko 1986; Campbell 1986a). While tagging lobsters (Campbell and Brattey 1986; Campbell 1986a), large aggregations of berried females were found in shallow waters off North Head, Grand Manan (Fig. 1) during the summers of 1982–93. The purpose of this paper is to show that even in adjacent areas the relative abundance of berried female and male lobsters can vary considerably, suggesting that the certain physical attributes of some areas may be preferred by berried female *H. americanus* for hatching and extruding eggs.

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Materials and Methods

Size frequencies, sex ratios, and proportion of berried females in trap catches were obtained by sampling lobsters at sea during research trapping surveys off North Head during August and September 1982, and August 1983. Traps had entrances large enough to allow entry of large mature lobsters (Campbell and Duggan 1980). Fresh frozen fish was used as bait with an average of three (range 1–8) soak days between trap hauls. The five areas sampled (Fig. 1) had the following substrate types and depth ranges: (A) sand-clay sheltered harbour, 1–22 m; (B) coarse gravel with heavy boulders, 11–23 m; (C) ledge bedrock with coarse gravel and a few sand-clay patches, 15–37 m; (D) ledge bedrock with large boulders, 18–43 m; and (E) mud, 64–87 m. There was a considerable tidal current in area A; water depths ranged 1–8 m.

Eggs of berried females were examined and classified as "old" with developed embryos about to hatch and as "new" recently extruded eggs with no embryo or eye pigmentation. Female lobsters carry their eggs externally for 9–12 mo. Egg extrusion and hatch occur mainly during August–September off Grand Manan (Campbell 1986a). Sex ratios were calculated by dividing the total number of males by the total number of lobsters ≥81 mm carapace length (CL). Percentage size frequen-

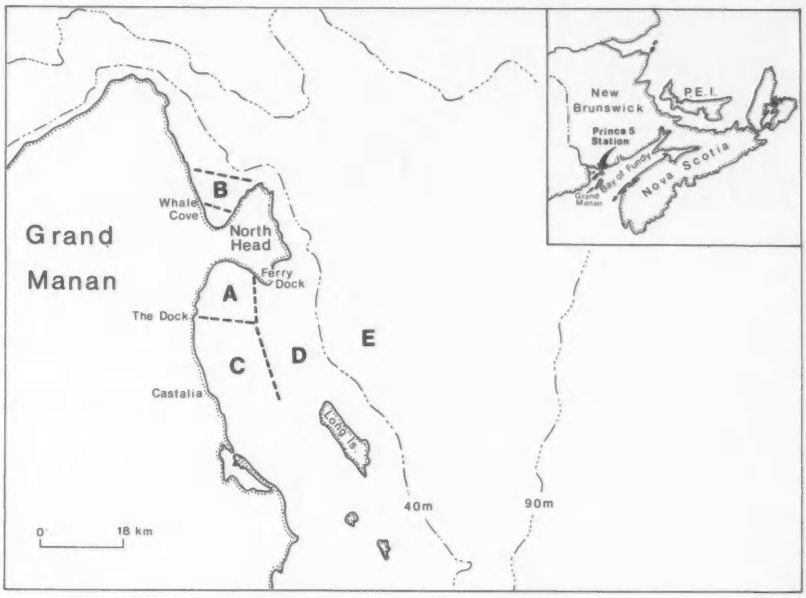

FIG. 1. Areas sampled off Grand Manan.

cies were determined by dividing the number of lobsters per 1 mm CL group by the total of all males, all females, or all berried females.

Differences between areas for the mean number of berried females per 100 trap hauls were determined using a one-way Analysis of Variance and Student-Newman-Keuls (SNK) test (Nie et al. 1975) after the data were transformed using $\log_{10}(x + 1)$.

The catch per trap information must be considered only as a relative index of lobster density because bias can be introduced with trap data. Trap catching efficiency could vary from location to location and time to time due to different activity levels of lobsters related to temperature changes (McLeese and Wilder 1958), changes in density, dispersion, and physiological condition of the lobsters (Krouse and Thomas 1975; Elner 1980).

During 23–29 September 1982, lobsters were collected by SCUBA divers in 52 randomly chosen 100-m^2 transects sampled 1 m on both sides of a 50-m rope line per transect in area A. Only area A was sampled by SCUBA because of the relative ease in catching lobsters in shallow, clear water with a sand–clay substrate without rocks and large seaweed to impede visibility. Sex, CL, and egg condition were recorded. All berried females caught by traps and SCUBA divers from all areas were each tagged with a sphyrion anchor tag (Scarratt and Elson 1965) and released within 10 min after removal from the water and within 50 m of capture. SCUBA diving was also used to randomly search for lobsters in area A during March 1983.

The largest diameter of each bowl-shaped depression in the substrate and the CL of 32 berried females each occupying a depression were measured under water in area A. The relationship between lobster CL and depression diameter was estimated using linear regression analysis (Nie et al. 1975).

Temperature profiles at different depths (surface, 10 m, and 65–75 m) were obtained from Prince Station 5 (44°56′N, 66°51′W) during summers 1982–83 (data from St. Andrews Biological Station, N.B., Canada) and from the surface and bottom from some areas during the middle of each month of sampling. From these data the average water temperature was extrapolated for the mean bottom water depth of each area.

Results

Trapping

The majority (94%) of lobsters caught off North Head were larger than 94 mm CL (Fig. 2). The largest male and female were 215 and 220 mm CL, respectively, and the smallest and largest berried female were 90 and 197 mm CL caught during summers 1982–83 (Fig. 2). The size ranges and mean CL of berried females were similar between all areas. However, there were consistently more berried females caught in traps from area A than any of the other areas during August–September 1982 and August 1983 (Table 1). There was a preponderance of berried females compared with unberried females and males in area A, and fewer berried females in the deeper areas C, D, and E (Table 1). The percentage berried females with new eggs was higher and more berried females occurred earlier in the shallow areas A and B compared with the deeper areas C, D, and E. The shallow areas A and B tended to have warmer water than the deeper areas (Table 1).

Diving Observations

From 52 transects, an average 2.327 berried females/100 m^2 (SE = ±0.039) were observed in area A by diving. The majority (98.3%), $N = 121$) had new eggs and 96% of the total females were berried, while only one of 127 lobsters collected was a male. The median CL for berried females caught by both traps and diving during September 1982 was 131 mm. No lobsters were found in area A during March 1983.

Male and female lobsters were observed in symmetrical bowl-shaped depressions in the sand–clay substrate, (one lobster per depression) similar to those observed from inshore and offshore

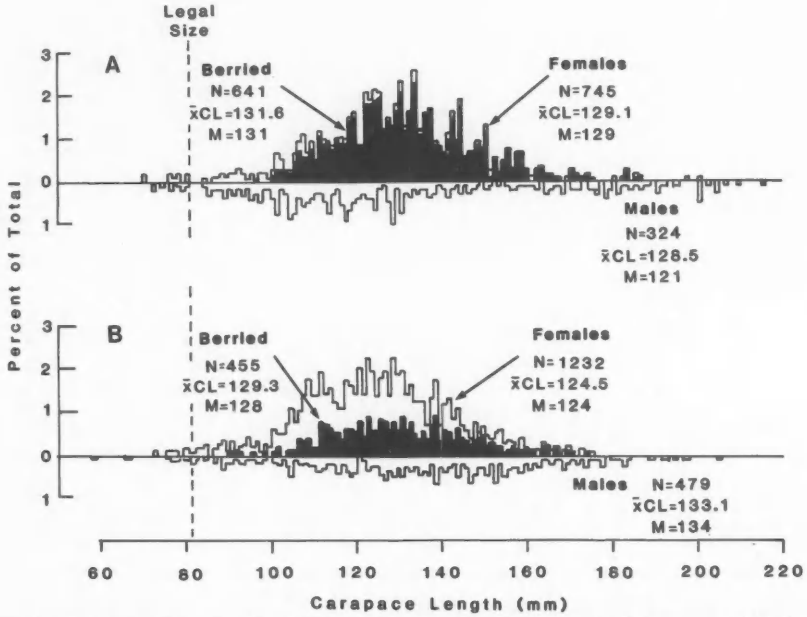

FIG. 2. Size frequencies of berried females, all female and male lobsters caught by traps off North Head, Grand Manan (all areas combined) during (A) September 1982 and (B) August 1983. N = total number, $\bar{x}CL$ = mean carapace length and M = median carapace length in millimetres.

TABLE 1. Number of berried females per 100 trap hauls and sex ratios of lobsters caught in different areas near Grand Manan, by month during summers 1982 and 1983. Only lobsters ≥ 81 mm CL considered. Means not followed by same letter in column are significantly different ($p < 0.05$, SNK-test).

Data	Area	Mean number of berried females per 100 trap hauls	Percent of total berried females with new eggs	Percent berried females of total females	Percent males of total lobsters	Number of		No. of trap hauls	Bottom temperature (°C)
						Berried females	Total lobsters		
August 1982	A	64.4[b]	70.0	71.6	19.4	342	593	531	11.0
	B	32.4[d,e]	44.6	52.0	37.2	93	285	287	11.0
	C	29.2[d,e]	30.2	35.0	39.2	63	296	216	10.6
	D	26.6[d,e]	34.0	43.6	46.3	51	218	192	9.4
	E	0	—	—	—	0	0	48	9.3
Sept. 1982	A	90.0[a]	92.0	94.9	4.7	388	450	431	11.8
	B	56.9[b,c]	89.7	81.7	40.2	107	219	188	11.7
	C	30.7[d,e]	77.3	74.2	50.8	66	181	215	11.2
	D	25.9[e]	60.0	74.8	46.8	80	201	309	11.2
August 1983	A	88.3[a]	54.2	55.6	11.2	212	429	240	11.2
	B	45.8[c,d]	49.5	36.1	28.1	99	381	216	11.2
	D	20.4[e]	11.2	25.3	34.7	98	513	480	10.6
	E	17.7[e]	5.3	26.4	36.0	38	225	215	10.3

areas of New England (Cooper and Uzmann 1980, their figure 6) and lobsters held in tidal pounds off Grand Manan (A. Campbell, pers. observ.). The lobsters excavate the depressions by "bulldozing" — pushing the sand–clay out of the depressions with their chelipeds. Many lobsters had white sediment adhering to a third of the outer area of each cheliped indicating bulldozing activity. The CL of the berried females (X, in mm) and the diameter of the depression (Y, in cm) ($Y = 29.3 + 0.34X$, $r = 0.56$, $N = 32$) were significantly correlated ($p<0.01$).

The berried females probably did not stay in area A for more than a few weeks. Of the berried lobsters tagged ($N = 893$) in area A during summer 1982, about 10% were recovered (usually by traps) in the same area within a mean 18 d (range 1–55 d). Underwater observations of tagged berried females after release indicated that the majority moved immediately to deeper water. Locomotion was forward walking with abdomen and telson curved under the carapace.

Discussion

Some of the highest numbers of berried females per trap haul were recorded by this study for the shallow waters of North Head compared with other areas of the Bay of Fundy and coastal southwestern Nova Scotia during the August–September period

(Campbell 1984, 1986b; Campbell and Pezzack 1986). Mature lobsters can occur in large numbers in the relatively shallow and warm offshore waters of Georges Bank and Browns Bank during summer (Cooper and Uzmann 1980; Pezzack 1983). Area A probably represents an ideal coastal area for berried lobsters to extrude and hatch eggs because the shallow waters mix with warm surface waters, and the sheltered area is normally safe from major storm surges, allowing the accumulation of soft sand–clay substrate. Only a few kilometres south of North Head are the productive waters of southern Grand Manan where most of the commercial lobster catch for this area is taken during the November–June fishing season and, yet, few berried females are found there (Templeman 1936; Campbell and Duggan 1980). Whether these aggregations are unique to Grand Manan or generally occur in other coastal areas throughout the range of *H. americanus* is unknown. Mature lobsters are known to move to warm shallow waters in the Bay of Fundy and offshore areas during summer to molt, extrude and hatch eggs (Cooper and Uzmann 1971; Campbell 1986a; Campbell and Stasko 1986). Thus, the transitory nature of these aggregations could be attributed to the migratory habits of mature lobsters and their physiological requirements for warmer habitats in an area such as Grand Manan where waters are generally cold for most of the year (Campbell 1986a; Campbell and Stasko 1986). Warmer temperatures compared with cooler temperatures during summer help to speed up the process of egg development and hatching (Templeman 1940; Perkins 1972). Whether other factors of a biological nature such as predation or food supply had an influence on the distribution of berried females is unknown. By November–December 1982, most berried females were caught in traps set at 37–144 m depths with no mature lobsters caught in the shallow waters of area A (A. Campbell, unpubl. data; Campbell 1986a).

The preponderance of berried females and lack of males in the shallow waters, such as area A, might be attributed to the aggressive behaviour of berried females (especially during egg hatching and/or extrusion) (A. Campbell, pers. observ.) or to sexual differences in the timing of dispersal movements (Campbell and Stasko 1986). Also, berried females and mature unberried females caught by diving or trapping in this study were in the hard-shelled intermolt stage. Females that were molting, soft-shelled and/or mating probably shelter under rocks or in burrows where mature males would have territories (Atema 1986; Karnofsky and Price 1989).

The aggregations of berried *H. americanus* females in this study were not as dense as those found for the rock lobster, *Jasus edwardsii*, in waters off New Zealand (McKoy and Leachman 1982). However, the function of these aggregations may be similar since they occur in strong tidal water currents which would allow rapid dispersal of newly hatched larvae. Where lobster larvae hatched near North Head eventually settle is unknown. The larvae could be swept by currents along the coast of Maine or caught in eddies in the productive grounds of the southern coast of Grand Manan (Bumpus and Lauzier 1965).

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Recruitment Mechanisms of Bloater in Lake Michigan: an Analysis of the Predatory Gauntlet

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Laboratory experiments were used to evaluate the potential importance of size-dependent predation on bloaters through the first 1–2 mo after hatching. Of the potential predators encountered by bloater eggs and larvae during their hypolimnetic phase, only sculpins appear important. Sculpin feeding rate on eggs increased when egg or larval density was high. The presence of amphipods as alternative prey enhanced predation on eggs when on cobble, but reduced predation when eggs were on sand. Sculpin feeding rate on larvae decreased when amphipods were present. All three epilimnetic predators, yearling alewife, smelt, and bloaters, readily ate bloater larvae. The presence of zooplankton as alternative prey reduced predation on larvae by smelt and bloaters, but not by alewives. Capture success was strongly size-dependent for all three predators. All three species exhibited the same exponential decline in handling time with increasing predator:prey ratio. Computer simulations using results from these experiments show that when mortality is size-dependent, small changes in growth rate can have dramatic effects on survival. Sculpins and alewife are likely to be the most important predators in determining bloater recruitment in Lake Michigan.

Grâce à des expériences en laboratoire, on a pu évaluer l'importance potentielle de la prédation en fonction de la taille exercée sur le Cisco de fumage durant le premier et le deuxième mois suivant l'éclosion. Seul le Chabot paraît être un important prédateur parmi les prédateurs potentiels des oeufs et des larves du Cisco de fumage durant la phase hypolimnétique. Le taux de prédation par le Chabot s'accroît lorsque la densité des oeufs ou des larves est élevée. La présence d'amphipodes qui servent aussi de proies active la prédation sur les oeufs lorsque ces derniers se trouvent sur des galets, mais l'atténue lorsque les oeufs sont sur le sable. En présence d'amphipodes, les Chabots se nourissent moins de larves. Les trois prédateurs épilimnétiques, le Gaspareau d'un an, l'Éperlan et le Cisco de fumage, se nourissent sans peine des larves du Cisco. La présence de zooplancton conduit à une réduction de la prédation sur les larves par l'Éperlan et le Cisco, mais pas par le Gaspareau. Chez les trois prédateurs, le succès des captures dépend fortement de la taille. Les trois espèces ont manifesté la même baisse exponentielle dans la durée de traitement des proies en fonction du rapport croissant prédateur-proie. Il a été montré par des simulations sur ordinateur à partir des résultats obtenus que lorsque la mortalité est fonction de la taille, de petites variations du taux de croissance peuvent avoir des effets très accentués sur la survie. En toute probabilité, le Chabot et le Gaspareau sont les prédateurs les plus importants pour la détermination du recrutement des Ciscos de fumage dans le lac Michigan.

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The complexity of interacting biotic and abiotic mechanisms is a major obstacle to understanding recruitment of fishes. Rice et al. (1987b) attacked this problem for Lake Michigan bloater (*Coregonus hoyi*) by comparing characteristics of "survivors" through the first 1–2 mo of life with those of larvae at earlier life history stages. Their results suggested that survival was affected by selective mortality during both the egg incubation period and the first few weeks after hatching. Predation has been suggested as an important mechanism constraining recruitment (Crowder 1980; Hunter and Kimbrell 1980; Hunter 1981), and the interaction between larval fish and their predators is strongly size-dependent (Miller et al. 1988).

In Lake Michigan, the distribution of bloater eggs and yolk-sac larvae in the hypolimnion is overlapped by that of deepwater sculpin (*Myoxocephalus thompsoni*), and to a lesser extent that of slimy sculpins (*Cottus cognatus*) (Wells 1968). Both species eat bloater eggs (Wells 1980). Adult bloaters occur at the same depths as bloater eggs and larvae during spring. Adult alewives (*Alosa pseudoharengus*) occur with the eggs over the winter,

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but appear to move inshore before bloater larvae hatch (Wells 1968).

Once bloaters move to the surface, the only potential predators they are likely to encounter are juvenile alewives, juvenile bloaters, and rainbow smelt (*Osmerus mordax*). Alewives and smelt tend to be pelagic in near-surface waters and consume fish larvae (O'Gorman 1974; Brandt et al. 1987). Historically, bloaters spent their first 3 yr in the epilimnion, but recently have tended to switch to the bottom after their first year (Crowder and Crawford 1984). Other possible predators in the epilimnion of Lake Michigan are not likely to consume bloaters. Juvenile salmonines are concentrated near shore and feed primarily on terrestrial insects (Jude et al. 1987). A variety of cyclopoid copepods overlap spatially with larval bloater but appear to consume fish larvae that are smaller than 8 mm (Hartig et al. 1982). Bloater larvae hatch at approximately 10 mm and thus are relatively invulnerable to these copepod predators.

Our goal in this study was to evaluate the potential impact of size-dependent predation on bloater survival, for the major potential predators encountered by bloaters from spawning through the first 1–2 mo after hatching. We conducted laboratory experiments with each of the potential predators on bloater eggs and larvae, both with and without alternative prey, and at different prey densities, to determine the potential impact of predation on bloater survival and recruitment. Further, we tested the hypothesis that these predator–prey interactions are size-dependent, and evaluated the effects of growth rate on size-dependent predation mortality.

Materials and Methods

Lake Michigan water was pumped from an offshore station and temperature was controlled by cooling water in header tanks located above the experimental tanks and adjusting the flow rates to obtain the desired temperature. Fish were either reared in the laboratory from eggs (bloaters) or collected from Lake Michigan and allowed to acclimate to laboratory conditions for 2–3 mo prior to experiments (smelt, alewife, and sculpins). Bloater larvae were reared from eggs collected from ripe Lake Michigan females in February 1985 and 1986. Predators were offered the prey species to be used in the experiments for at least 1 wk prior to the experiments.

Hypolimnetic Feeding Trials

Feeding rates of slimy sculpin (86 ± 7.5 mm, mean total length (TL), TL + standard deviation, SD), adult alewives (157 mm TL ± 14.4 mm), and adult bloater (150 mm TL ± 20.8 mm SD) on bloater eggs were determined under simulated hypolimnetic conditions (total darkness, 4°C). Because we were unable to collect adequate numbers of deepwater sculpins, we used slimy sculpins and assumed responses of both species would be similar. Similarities in feeding morphology and diet of these two species make this assumption tenable (Kraft and Kitchell 1986). Experiments with sculpins were conducted in a section of the laboratory completely surrounded by black plastic. Individual predators were placed in feeding chambers (30 × 14.5 × 20 cm deep), also surrounded by black plastic, and held without food for 5 d. Treatments consisted of two densities of bloater eggs (low: 218 eggs or 0.5 eggs·cm^{-2}; high: 2180 eggs or 5 eggs·cm^{-2}) paired with two substrates (sand and 5 to 7 cm cobble), either alone or with the amphipod *Gammarus lacustris* (density = 0.5·cm^{-2}, mean length = 6.4 ± 1.5 mm) as alternative prey, in a 2 × 2 × 2 factorial design with eight replicates (Table 1). Density estimates for bloater eggs in Lake Michigan are unavailable but Rupp (1965) reported rainbow smelt densities averaging 1.8–3.0 eggs·cm^{-2} with some values as high as 12 cm^{-2}. In Lake Michigan, *Pontoporeia* densities average 0.3–0.7 cm^{-2} (McDonald et al. 1990).

Because we could not obtain adequate numbers of *Pontoporeia*, a major component of both slimy and deepwater sculpin diets (Wells 1980), we used *Gammarus*. The purpose of using this amphipod was to allow us to estimate the feeding rate of sculpins when an alternative prey was present.

Gammarus were collected from a local spring and kept in 100-L tanks at 4°C. Prior to a feeding experiment, 218 *Gammarus* were counted and placed in 200-mL plastic containers with netting affixed to one end, and returned to the larger tanks. A representative sample was preserved and later measured to determine the size distribution used on a given day. On the day of an experiment, prey of the appropriate treatment were placed in 32 chambers containing an individual starved sculpin. The sculpins were fed for 30 min and then removed from the chamber, anesthetized with MS222 (1 g·L^{-1}), and sacrificed for stomach content analysis. All eggs and *Gammarus* in the stomach of each fish were counted immediately and preserved. These experiments were repeated on four dates, resulting in 16 sculpins in each of the eight treatments.

In 1985, a limited set of trials with adult bloaters was conducted using the same experimental system and conditions, except that the chambers were doubled in size (Table 1). The treatments used were high egg density (5·cm^{-2}) with no alternative prey, on sand or cobble substrate; each treatment was replicated six times. These 12 trials were also repeated with the lights on.

In 1986, trials were conducted in larger (200-L) oval tanks, again at 4°C and in total darkness (Table 1). These treatments used low egg density (0.5·cm^{-2}) and sandy substrate, both with and without *Gammarus* (0.5·cm^{-2}) as alternative prey. Six adult bloaters were used in each tank because our observations suggested that these fish may feed more readily in a group. Data for the six predators were averaged and treated as one measurement; each treatment was replicated two times. Two trials were conducted with bloaters under low light conditions; a single 15-W light bulb suspended 1 m above the tank provided less than 5 lx of illumination. These low light intensity trials were conducted using low egg densities, and sand substrates in the absence of alternative prey.

The potential for predation on bloater eggs by adult alewives was evaluated using two groups of 20 predators each, held in two oval, 200-L, glass-front tanks (Table 1). The fish were held at 4°C for 2 wk, and not fed for 72 h prior to the observation period. One tank was kept covered with black plastic throughout the trial, and the other was maintained on a 12L:12D photoperiod. At the start of the trial, 8000 eggs (2·cm^{-2}) were added to each tank. One hour after the eggs were added, four fish were removed from the covered tank, anesthetized, measured, and their stomach contents examined. An additional four fish were removed for stomach analysis every 24 h, over 4 d. One hour before the final group of fish was sacrificed, flake food and frozen adult brine shrimp (*Artemia*) were added to the tank to assure that predators were hungry and likely to consume food.

Alewives in the lighted tank were observed for 15 min after the eggs were introduced, to see if any feeding occurred. After 3 h, four fish were removed for stomach analysis. Because

TABLE 1. Design of hypolimnetic and epilimnetic predation experiments. The mean length and year experiments were conducted is listed below each predator. Egg, yolk-sac larvae (Y-S), or 12-mm larval (Larv) bloaters were prey. Prey density is given in numbers·cm^{-2} for egg trials, and numbers·L^{-1} for Y-S and Larv trials. We simulated hypolimnetic conditions for egg and Y-S trials and epilimnetic conditions for Larv trials. Number pred is the number of predators per experimental tank. Substr refers to substrate type (– indicates no substrate was used). Alternate prey were none (no), *Gammarus* (G), or zooplankton (Z). Tank volume is in litres. Light conditions were: dark — total darkness, room — room illumination (59 lx), and low — <5 lx.

Predator	Prey stage	Prey density	Number pred.	Substr.	Alt. prey	Tank volume	Temp. (°C)	Light cond.	Number of reps
Hypolimnetic trials									
Sculpin	Egg	0.5	1	Sand	no	9	4	dark	8
(86mm)	Egg	0.5	1	Sand	G	9	4	dark	8
1986	Egg	0.5	1	Cobble	no	9	4	dark	8
	Egg	0.5	1	Cobble	G	9	4	dark	8
	Egg	5.0	1	Sand	no	9	4	dark	8
	Egg	5.0	1	Sand	G	9	4	dark	8
	Egg	5.0	1	Cobble	no	9	4	dark	8
	Egg	5.0	1	Cobble	G	9	4	dark	8
Sculpin	Y-S	1.67	1	Sand	no	9	4	dark	8
(86mm)	Y-S	1.67	1	Sand	G	9	4	dark	8
1986	Y-S	1.67	1	Cobble	no	9	4	dark	8
	Y-S	1.67	1	Cobble	G	9	4	dark	8
	Y-S	16.7	1	Sand	no	9	4	dark	8
	Y-S	16.7	1	Sand	G	9	4	dark	8
	Y-S	16.7	1	Cobble	no	9	4	dark	8
	Y-S	16.7	1	Cobble	G	9	4	dark	8
Alewife	Egg	2.0	20	Sand	no	200	4	room	2
(157mm)	Egg	2.0	20	Sand	no	200	4	dark	2
1985									
Bloater	Egg	5.0	1	Sand	no	18	4	dark	6
(150mm)	Egg	5.0	1	Sand	no	18	4	room	6
1985	Egg	5.0	1	Cobble	no	18	4	dark	6
	Egg	5.0	1	Cobble	no	18	4	dark	6
Bloater	Egg	0.5	6	Sand	no	200	4	dark	2
(150mm)	Egg	0.5	6	Sand	G	200	4	dark	2
1986	Egg	0.5	6	Sand	no	200	4	low	2
Bloater	Y-S	16.7	1	Sand	no	18	4	dark	6
(150mm)	Y-S	16.7	1	Sand	no	18	4	room	6
1985	Y-S	16.7	1	Cobble	no	18	4	dark	6
	Y-S	16.7	1	Cobble	no	18	4	room	6
Bloater	Y-S	0.75	8	Sand	no	200	4	dark	3
(150mm)	Y-S	0.75	8	Sand	G	200	4	dark	3
1986	Y-S	0.75	8	Sand	no	200	4	low	3
	Y-S	0.75	8	Sand	G	200	4	low	3
Epilimetic trials									
Alewife	Larv	0.05	10	—	no	400	18	room	3
(92mm)	Larv	0.05	10	—	Z	400	18	room	3
1986	Larv	0.25	10	—	no	400	18	room	3
	Larv	0.25	10	—	Z	400	18	room	3
	Larv	0.75	10	—	no	400	18	room	3
	Larv	0.75	10	—	Z	400	18	room	3
Bloater	Larv	0.05	10	—	no	400	18	room	3
(65mm)	Larv	0.05	10	—	Z	400	18	room	3
1986	Larv	0.25	10	—	no	400	18	room	3
	Larv	0.25	10	—	Z	400	18	room	3
	Larv	0.75	10	—	no	400	18	room	3
	Larv	0.75	10	—	Z	400	18	room	3
Smelt	Larv	0.05	6	—	no	400	12	room	3
(57mm)	Larv	0.05	6	—	Z	400	12	room	3
1986	Larv	0.25	6	—	no	400	12	room	3
	Larv	0.25	6	—	Z	400	12	room	3
	Larv	0.75	6	—	no	400	12	room	3
	Larv	0.75	6	—	Z	400	12	room	3

Crowder and Binkowski (1983) found that alewives preferred prey in the water column, we circulated eggs in the water for 15 min by siphoning eggs off the bottom and releasing them at the surface, while again observing behavior of the alewives. On subsequent days fish were observed for the first 15 min after the lights were turned on, and also during the second 15 min while the eggs were recirculated.

Predation experiments were also conducted with sculpins and adult bloater feeding on bloater yolk-sac larvae (12.4 mm TL ± 0.8 mm SD) under simulated hypolimnetic conditions. Trials with sculpins were conducted in the same tanks following the same protocol used for the egg predation trials. Eight treatments were used in a 2 × 2 × 2 factorial design, with sand or cobble substrate, low (15 larvae, $1.67 \cdot L^{-1}$) or high (150 larvae, $16.7 \cdot L^{-1}$) larval density, and with or without *Gammarus* ($0.5 \cdot cm^{-2}$) as alternative prey. Each treatment was replicated eight times (Table 1).

In 1985, trials with adult bloaters were conducted in the smaller chambers (30 × 29 × 20 cm deep), using high larval density ($16.7 \cdot L^{-1}$) with no alternative prey, on sand or cobble substrate; each treatment was replicated six times, both in darkness and under room illumination. In 1986, trials with adult bloaters were conducted in the 200-L oval tanks, using two treatments, 150 larvae per tank ($0.75 \cdot L^{-1}$) both with and without *Gammarus* ($0.5 \cdot cm^{-2}$) as alternative prey. Eight bloaters were used in each tank; data for the eight predators were averaged, and the experiment was replicated twice. Two additional trials were also conducted under conditions of low light.

Epilimnetic Feeding Trials

The ability of three epilimnetic predators (yearling smelt (57 ± 8.7 mm), alewife (92 ± 11 mm), and bloater (65 ± 7.8 mm)) to feed on 12-mm bloater larvae (the size at which bloater larvae reach the surface; Rice et al. 1987b) was examined in large (400-L) circular tanks under room illumination (59 lx). Three densities of larvae (50, 250, and $750 \cdot m^{-3}$) were paired both with and without natural densities (35–$98 \cdot L^{-1}$) of zooplankton in a 3 × 2 factorial design repeated three times on separate dates. Densities of bloater larvae in Lake Michigan averaged 35 individuals$\cdot m^{-3}$ with peak densities of $90 \cdot m^{-3}$ (Rice et al. 1987b). We used higher densities in some trials to estimate the potential maximum feeding rates of each of the predators.

For the alewife and bloater experiments, 15 individuals were placed in one of the tanks at 18°C and held without food for 48 h. The day the experiment was conducted, the appropriate number of larvae (20, 100, or 300) were placed in a 250-mL container and gently placed into the feeding tanks. Predators were allowed to feed for 5 min and then 10 individuals were removed, anesthetized in MS-222 and sacrificed. Total length and weight of each individual was measured, and stomach contents were examined and counted. Data for the 10 fish were treated as one replicate. In feeding trials where zooplankton were used as alternative prey, both zooplankton and larvae were poured into a 2.6-L plexiglas cylinder plugged with a rubber stopper in one end, and placed in the experimental tank. The rubber stopper was then removed, and the trial began. On each day 50 larvae from the stock tank were preserved in 10% formalin and later measured.

Feeding experiments with smelt were conducted at 12°C for 30 min because the smelt did not survive well at 18°C. The treatments were identical to the alewife and bloater experiments except only six smelt were used in the tank at one time.

On the morning the trial was conducted, zooplankton were collected with a 150-μm mesh plankton net from Lake Mendota, Madison, Wisconsin. Three equally-timed horizontal tows were taken from a depth of 1 m and placed in individual 20-L plastic buckets. The length of tow varied among dates so that approximately equal abundances of zooplankton were collected. Just prior to a feeding trial the zooplankton from one 20-L bucket were placed in the 2.6-L plexiglass cylinder. Two 20-mL aliquots of the zooplankton concentrate was preserved in 4% formalin for later identification. After each feeding trial, two samples (1.75 L) were taken from the experimental tank by lowering the 2.6-L plexiglass cylinder onto a rubber stopper placed on the bottom of the tank. The zooplankton in each of these samples were preserved in 4% formalin for later identification.

Behavioral observations

The ability of the three epilimnetic predators to capture and handle larval and juvenile bloaters was estimated with a series of observational feeding trials using four sizes of bloater prey (13.2, 19.9, 25.5, 31.5 mm TL) in 200-L oval tanks with a plexiglass front window (40 × 30 cm). Feeding trials with alewives and bloaters as predators were conducted at 18°C with six predators per tank and trials with smelt at 12°C with 10 predators per tank.

To determine capture success, one researcher would submerge a 200-mL opaque container with 20 bloater larvae of the appropriate size into the observation tank while another observer kept the predators to one side of the aquarium with a net. After the bloater prey were released, the net was removed and the number of attempted attacks and successful captures were recorded. An attack was defined as anytime a predator oriented to and chased a potential prey. A successful capture was defined as any time a prey entered the mouth of a predator. Each treatment was repeated five times on consecutive days. The number of capture attempts used in each probability of capture estimates ranged from 7 to 62, with a median of 28. Each day, 10 larvae were measured to the nearest 0.1 mm TL using a dissecting microscope fitted with an ocular micrometer.

Handling times were determined in separate feeding trials approximately 6 h after the capture success trials. A few larvae of appropriate size were poured into the tank. A stopwatch was started when a successful capture occurred and stopped when the swallowing motions of the predator ceased and search behavior resumed. Because handling times tended to increase as more larvae were consumed, only the first three handling time observations from a feeding bout were used in subsequent analyses. The three values were averaged, and repeated on five consecutive days. A tape recorder was used to record observations.

Results

Hypolimnetic Feeding Trials

Sculpins consumed bloater eggs in all treatments. A three-way ANOVA (data transformed log $x + 1$) revealed that both egg density and substrate (sand, cobble) had a significant effect on the consumption of bloater eggs by sculpin (Fig. 1). Sculpins consumed more eggs at the high egg density (mean = 31.2) than when low densities of eggs were offered (mean = 8.5), and a greater number of eggs were consumed on the sand substrate

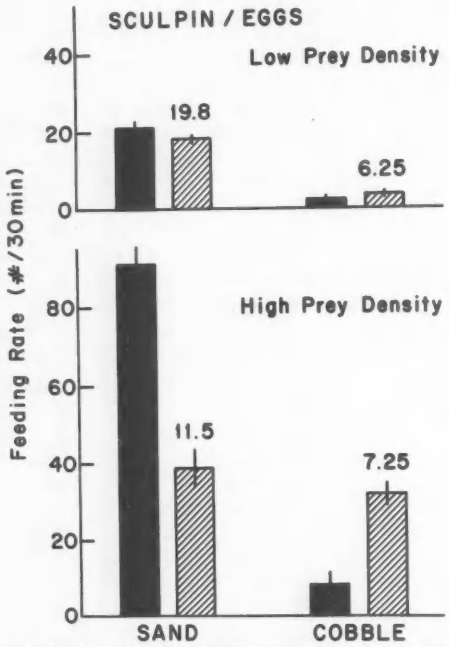

FIG. 1. Mean (±SE) number of bloater eggs consumed by sculpins in laboratory feeding trials conducted with two substrates (sand and cobble), two prey densities (low, $0.5 \cdot cm^{-2}$; high, $5 \cdot cm^{-1}$), in either the presence (hatched bars) or absence (solid bars) of alternative prey (*Gammarus*). Numbers over hatched bars show the mean number of *Gammarus* consumed during the feeding trial. A $2 \times 2 \times 2$ ANOVA of $\log(x+1)$-transformed data indicated significant effects of prey density ($F = 25.9$, df = 1,56, $p < 0.001$) and substrate ($F = 38.6$, df = 1,56, $p < 0.001$) and a significant interaction term between the presence of alternative prey and substrate ($F = 3.99$, df = 1,56, $p < 0.05$).

(mean = 36.2) than on cobble (mean = 7.5). The presence of *Gammarus* as alternative prey enhanced predation on bloater eggs on cobble substrates but reduced feeding on sand as evidenced by the significant interaction term between substrate and alternative prey.

Adult bloaters did not consume any bloater eggs when experiments were conducted in total darkness, regardless of the presence of alternative prey, the substrate type or container size used. No *Gammarus* were eaten in trials with alternative prey. Only one bloater ate any eggs (11) in the trials conducted under room illumination in the small chambers. In four trials conducted in the 200-L tanks under dim light with low egg densities on sand substrate, only three of 24 adult bloaters tested consumed eggs. Two fish consumed one egg and another consumed three eggs.

Adult alewives did not eat bloater eggs in either dark or lighted conditions. However, fish in the lighted tank fed readily on flake food and frozen brine shrimp at the end of the observation period. There was no evidence of brine shrimp or flake food in the stomachs of fish taken from the dark tank.

Sculpins consumed bloater yolk-sac larvae under all experimental conditions. Sculpins ate significantly more larvae at high larval density (mean = 22.0) than at low density (mean = 2.11; Fig. 2), and the presence of *Gammarus* reduced the feeding rate of sculpins on both substrates (mean = 5.4 with *Gammarus*, 10.0 without *Gammarus*; Fig. 2). Although

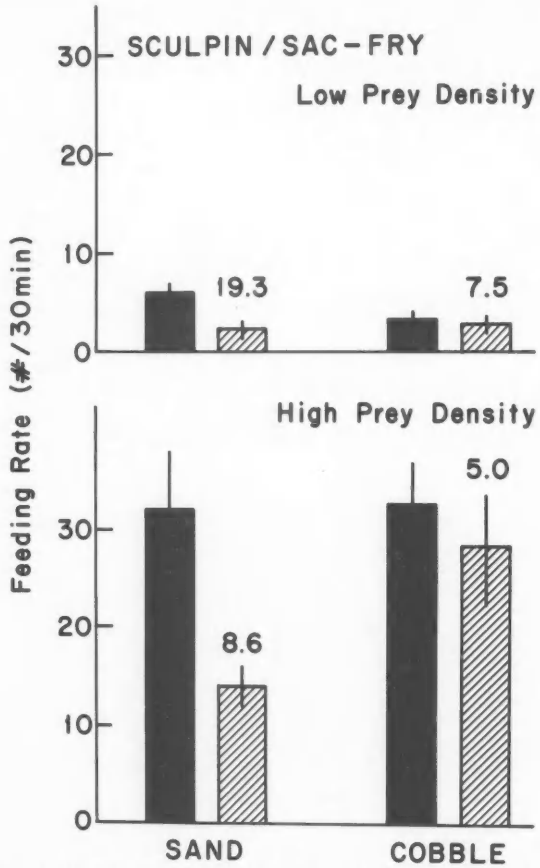

FIG. 2. Mean (±SE) number of bloater sac-fry larvae consumed by sculpins in laboratory feeding trials. Symbols as in Fig. 1. A $2 \times 2 \times 2$ ANOVA indicated significant effects of prey density ($F = 101$, df = 1,56, $p < 0.001$) and the presence of alternative prey ($F = 7.23$, df = 1,56, $p < 0.05$) and a significant interaction term between substrate and the presence of alternative prey ($F = 4.87$, df = 1,56, $p < 0.05$).

substrate type had no effect on sculpin feeding rate, a significant interaction term between substrate and the presence of alternative prey indicates that the presence of *Gammarus* reduced feeding on yolk-sac larvae more on sand than on cobble substrate (Fig. 2).

Adult bloaters did not feed on bloater yolk-sac larvae in total darkness regardless of substrate type, container size, or the presence or absence of alternative prey. Alternative prey were also not eaten by bloaters in these trials. Two of 12 bloaters tested in the small chambers with the lights on ate larvae (one and seven), and bloaters tested in the 200-L tanks under low light conditions (<5 lx) also consumed some larvae (mean = 14.4, $n = 16$).

Epilimnetic Feeding Trials

Feeding rate of alewives increased significantly with larval density in trials both with and without zooplankton (MANOVA with date of experiment as a random factor, $F = 12.9$, df = 2,10, $p < 0.01$), reaching a mean of 3.7 bloater larvae per 5 min at

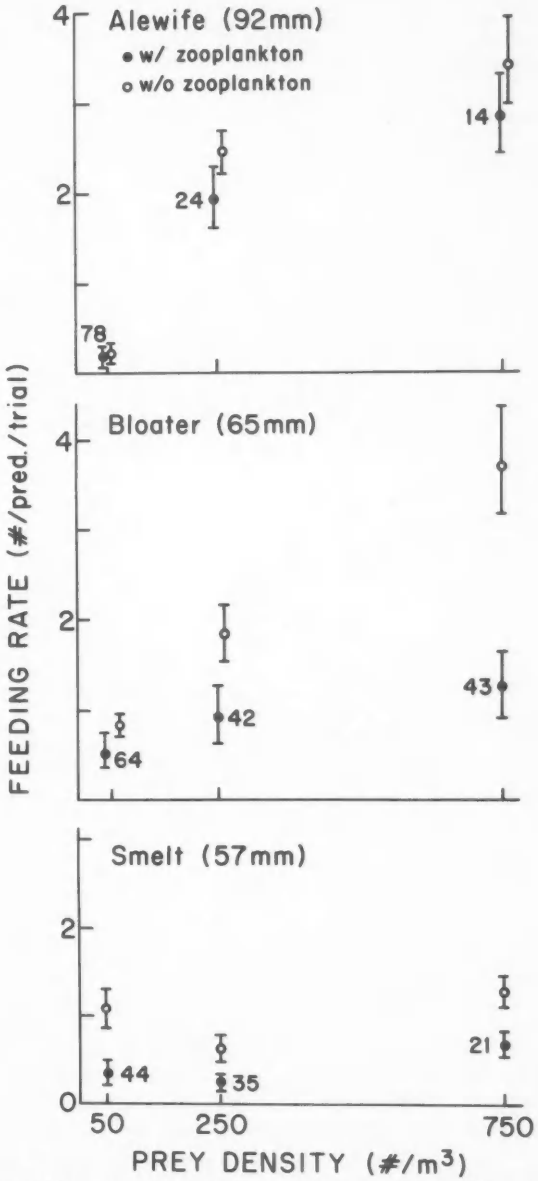

FIG. 3. Mean (± SE) number of larvae eaten per predator in epilimnetic feeding trials. Closed circles represent trials with zooplankton as alternative prey; open circles represent trials without zooplankton. Mean total length of predators are shown. The numbers next to each closed circle are the mean number of zooplankters consumed by predators in that treatment.

the highest larval densities (Fig. 3a). The presence of zooplankton did not affect predation rate of alewives on bloater larvae ($F = 0.29$, df = 1,10, $p > 0.60$). Rather, consumption of zooplankters decreased as larval density increased, indicating that alewives substituted bloater larvae for zooplankton when possible. The interaction term between larval density and the presence of zooplankton was not significant ($F = 1.10$, df = 2,10, $p > 0.40$).

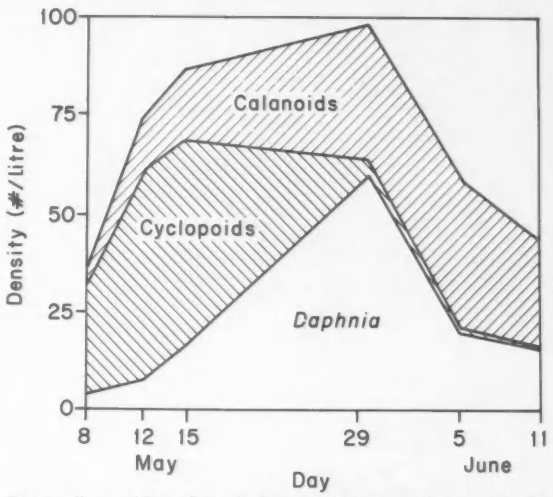

FIG. 4. Composition of zooplankton used as alternative prey in the epilimnetic feeding trials. The top line represents the total density of zooplankters.

Yearling bloaters consumed bloater larvae (12 mm) under all experimental conditions (Fig. 3b). Bloater feeding rate was significantly affected by larval density ($F = 16.2$, df = 2,10, $P < 0.001$) and the presence of zooplankton ($F = 15.4$, df = 1,10, $p < 0.01$). In contrast to yearling alewives, yearling bloaters consumed approximately equal numbers of zooplankters regardless of the density of larvae indicating that 65-mm bloaters consumed zooplankton even when larval fish were abundant. The interaction between larval density and the presence of zooplankton was not significant ($F = 2.47$, df = 2,10, $p > 0.10$).

Rainbow smelt consumed 12-mm bloater larvae, but not in high numbers (Fig. 3c). Density of larvae had no effect on smelt feeding rate ($F = 2.68$, df = 2,10, $p > 0.10$) probably because smelt became satiated after ingesting one–two larvae; 88% of smelt consumed three or fewer larvae. Two smelt consumed seven larvae but these individuals were larger (67 and 69 mm) than the mean length (57), suggesting that larger smelt would consume greater numbers of bloater larvae. The presence of zooplankton reduced feeding rate of smelt on bloater larvae ($F = 13.5$, df = 1,10, $p < 0.01$). The interaction between larval density and the presence of zooplankton was not significant ($F = 0.78$, df = 2,10, $p > 0.50$).

Densities and relative abundance of zooplankton used in these feeding trials varied (Fig. 4) with abundance of all zooplankters ranging from 35.3–97.9 organisms·L^{-1}. Cyclopoid copepods (primarily *Diacyclops thomasi*) were more abundant on the first three sampling dates and calanoid copepods (primarily *Diaptomus siciloides*) were most abundant on the last two dates. A large number of juvenile *Daphnia* (*D. pulex* and *D. galeata*) were present on May 29, resulting in *Daphnia* abundance of 60·L^{-1}. On this date the mean length of *Daphnia* was 0.76 mm compared with 1.06 for the other dates. Because feeding trials with each of the epilimnetic predators were conducted on three of the five dates, the variability in zooplankton abundance and composition was distributed across treatments.

Behavioral observations

Capture success of all three epilimnetic predators declined as length of larval bloater increased, falling from about 85% on

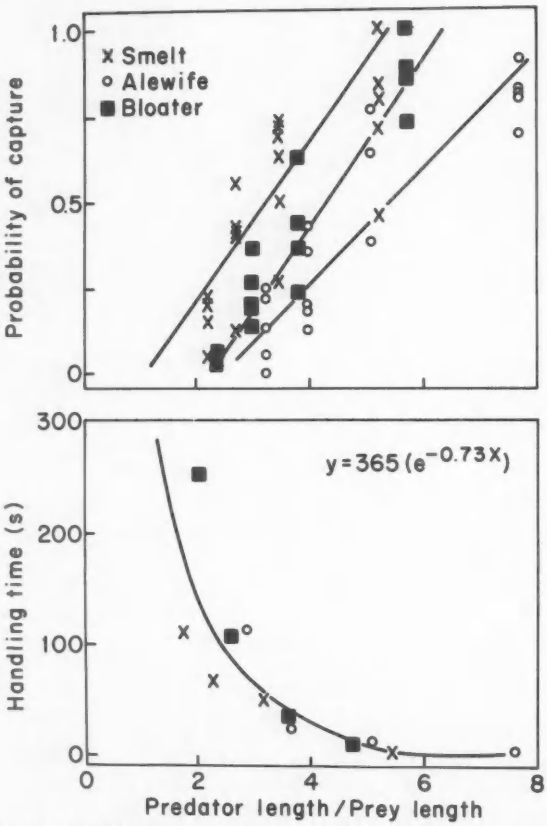

FIG. 5. (Top) Linear regression of probability of successful capture versus the predator:prey length ratio for each of the three epilimnetic predators. (Bottom) Mean handling time versus predator:prey length ratio for each of the epilimnetic predators. Linear regression of ln-transformed data indicated there were no significant differences among slopes for the three predators, so a single regression line was fitted to the data from all three predator species.

13.2-mm larvae to about 5% on 31.5-mm prey (Fig. 5, top). An ANCOVA using predator:prey size ratios as a covariate indicated significant differences among the three predators ($F = 25.2$, df = 2,53, $p < 0.001$). A multiple comparison of treatments using Bonferroni's procedure indicated that smelt had significantly higher capture success than bloaters ($F = 11.8$, df = 1,53, $p < 0.05$) and alewives ($F = 50.0$, df = 1,53, $p < 0.01$) in capturing prey; and that bloaters had higher capture success than alewives ($F = 16.2$, df = 1,53, $p < 0.01$).

Handling times for each predator declined exponentially with increasing predator:prey length ratio, and the relationship was the same for all three species (Fig. 5).

The relatively small size of experimental containers used in this study likely resulted in an overestimation of predation rates (de LaFontaine and Legget 1987). Thus, only comparisons of relative predation rates among hypolimnetic and epilimnetic predators are relevant.

Discussion

Field data on growth dynamics and survival of larval bloater suggested that both egg mortality and size-dependent mortality in the larval stage were important to recruitment of bloaters in Lake Michigan (Rice et al. 1987b). Of the three potential fish predators that coexist with bloater eggs and larvae in the hypolimnion of Lake Michigan, only sculpins appear to be significant predators. Prey density had a major effect on feeding rate for both eggs and larvae, but alternative prey and substrate types influenced predation rates. Cobble substrate reduced the feeding rate on eggs but not larvae. The presence of *Gammarus* consistently reduced feeding rate on larvae but not on eggs. Amphipods reduced the feeding rate of sculpins on bloater eggs on sand, but increased egg consumption on cobble. One possible explanation is that the presence of a mobile amphipod caused sculpins to move more frequently, thus increasing encounter rate with eggs. Cooper et al. (1985) reported similar results with mobile and non-mobile benthic prey.

Predation on bloater eggs and newly hatched larvae by adult bloaters and adult alewives in the hypolimnion of Lake Michigan is probably not important to recruitment processes of bloater. These potential predators did not consume bloater eggs or larvae under darkness and low temperature, even though they readily ate bloater larvae in an earlier study conducted in the light and at warmer temperatures (Rice et al. 1987a).

Differences in sensory capabilities may account for the differences in feeding among species. Sculpins have a well-developed lateral line and chemosensory ability for feeding in absolute darkness (Hoekstra and Janssen 1986). In our feeding trials, bloaters consumed few eggs and larvae and only under lighted conditions, indicating that bloaters may not be able to locate and capture these prey under conditions of total darkness.

Sculpins remain in the hypolimnion throughout the year, and hypolimnetic temperatures vary only a few degrees, so sculpin predation rate is probably constant when bloater eggs and larvae are present. Rice et al. (1987b) found that egg deposition in 1983, was only 57% of that in 1982, but larval recruitment was 2.4 times higher; hypolimnion temperatures were cooler in 1982 than in 1983, prolonging egg incubation for several weeks. This prolonged exposure to predators would be enough to account for the entire reversal in year class strength if the predation rate was only about 6% per day (Rice et al. 1987b). Within years, eggs that were spawned early in the season and thus exposed to egg predators longer were under-represented among the survivors sampled later in their first summer. Daily predation rates of 2–8%, coupled with the prolonged exposure of early-spawned eggs, could also account for this difference.

All three potential epilimnetic predators, yearling alewife, smelt, and bloaters, consumed bloater larvae under simulated epilimnetic conditions. Alternative prey (zooplankton) had substantially different effects on these three predators. The presence of zooplankton decreased feeding rate on bloater larvae by both bloater and smelt, but alewife feeding rate on bloater didn't change; instead, alewives consumed fewer zooplankton as larval bloater density increased. This suggests that among the common epilimnetic predators, only alewife tend to ignore zooplankton prey to search for larval fish, whereas bloater and smelt consume many zooplankters as well as fish larvae.

Yearling bloaters are now less abundant in the epilimnion of Lake Michigan, though they were pelagic planktivores for their first 3 yr before the alewife invasion (Crowder and Crawford 1984). Thus, predation by older bloaters might have been important to bloater recruitment, but is unlikely to be important now. Smelt did not consume many bloater larvae in our experiments, but were somewhat smaller than the available alewives and bloaters. Based on predator–prey size ratios, however, smelt

took significantly larger prey than did alewife or bloater. Although the presence of zooplankton reduced consumption of larval bloaters in our experiments, these results may not be applicable to situations where larger smelt are abundant (O'Gorman 1974). Thermal habitat preference of larger smelt (Brandt et al. 1980) suggest that they would not be abundant in the epilimnion and thus would have limited impact on bloater larvae.

In contrast to bloater and smelt, alewives ate substantial numbers of larvae and this consumption rate did not decline in the presence of zooplankton. Further, alewives in the size range we used are abundant in the epilimnion of Lake Michigan. Alewives are clearly prime suspects as predators on bloaters and other larval fishes (Brandt et al. 1987) in Lake Michigan.

Historical data indicates that alewife predation may have been a major factor in bloater recruitment dynamics. Of the 10 native Lake Michigan species with semi-pelagic eggs or larvae, nine became rare or extinct after alewives became abundant. All 11 native species with demersal eggs and larvae persisted after the alewife invasion (Crowder 1980). Bloater is the one species with semi-pelagic eggs or larvae that survived the alewife invasion. During the increase of alewife in Lake Michigan in the mid-1960s, bloater recruitment was poor (Brown 1972). Conventional wisdom suggested that reduced recruitment success was due to exploitative competition with alewife, in that alewife has a more efficient feeding mode than bloater (Crowder and Binkowski 1983). By the early 1970's, commercial fisheries for bloater were declining and the fishery was closed in 1976. Alewives began to decline in abundance in the mid 1970's, perhaps due to predation by stocked salmonids (Stewart et al. 1981; Kitchell and Crowder 1986) and have recently reached their lowest levels since the early 1960's. Bloaters began forming strong year classes again in 1977, despite the fact that the adult population was extremely reduced (Brown et al. 1987). Bloaters have continued to experience strong recruitment coincident with the alewife decline.

The similarity in size-dependence of handling time and capture success for the three epilimnetic predators we tested supports the idea that general predator–prey size relationships may explain the foraging behaviors of specific predators (Miller et al. 1988). For each of the predators examined, probability of capture declined from about 85% for 13-mm bloater to about 5% for 30-mm bloater. Even if captured, the long handling times observed indicate that feeding rates on 30-mm prey would be low for predators the size we used in these experiments. Overall, when bloaters reach 45–50% of the predator's length, they are no longer vulnerable; this size ratio agrees well with that observed for larval fish in general (Hunter 1981; Miller et al. 1988).

Growth rates and survival of larval fish are tightly integrated in the size-dependence of predation. Slowly growing fish not only are exposed to predation for longer periods of time (Shepherd and Cushing 1980; Werner and Gilliam 1984; Houde 1987) but also experience a higher probability of capture per encounter because of their smaller size. Because vulnerability changes rapidly with body size, small changes in growth rate can have dramatic effects on survival.

To illustrate the dynamics of this interaction we simulated the survival of a series of young-of-year bloater cohorts with different growth rates, exposed to size-dependent predation by 90-mm yearling alewives over a wide range of encounter rates. The simulations started with 12-mm bloaters and ran for 60 d, with growth rates ranging from 0 to 0.5 mm·d^{-1} and encounter

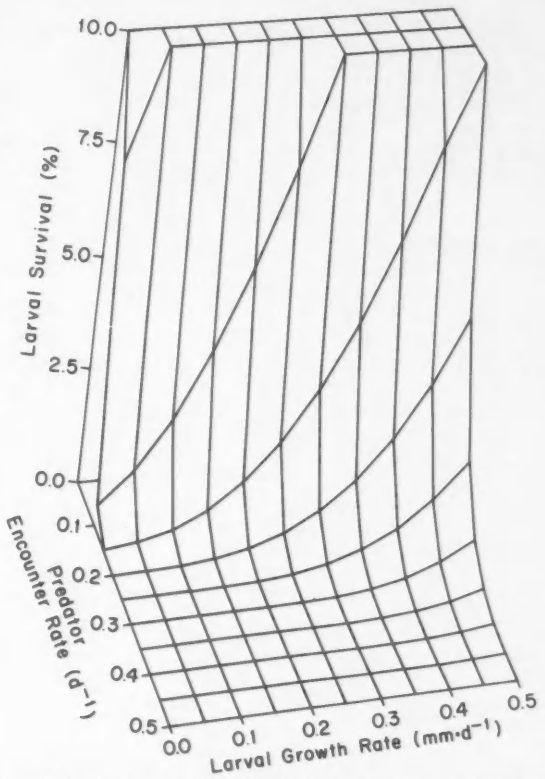

FIG. 6. Predicted survival over 60 d for bloater larvae exposed to size-dependent predation by 90-mm alewives, for a range of predator encounter rates and bloater growth rates. Initial bloater size was 12 mm. These simulations used the size-dependent probability of capture function for alewives from Fig. 5; predation was the only source of mortality. Survival values greater than 10% were truncated at 10% on the figure.

rates of 0 to 0.5·d^{-1}. Growth rates of larval bloaters in Lake Michigan are in this range or higher (Rice et al. 1987b). We have no realistic estimate of encounter rates in the field, but this range yields survival values from very high to very low, so actual encounter rates probably fall within this range. Probability of capture was determined each day from the predator:prey size ratio according to the relationship for alewive shown in Fig. 5. Predation was the only source of mortality.

Small changes in growth rate had major effects on survival over a wide range of predation intensity (Fig. 6). At low encounter rates (0.1·d^{-1}), a 0.1-mm·d^{-1} increase in growth rate increases survival over 60 d by 6–7%. With an intermediate encounter rate of 0.3·d^{-1}, a cohort growing at 0.3 mm·d^{-1} would have two orders of magnitude higher survival than one growing at 0.1 mm·d^{-1} (0.111 versus 0.001%). If growth rate increases to 0.5 mm·d^{-1}, survival increases another order of magnitude, to 1.261%. Houde (1987) has also demonstrated effects of growth rate on survival of this magnitude.

At high encounter rates, survival is always low, but small differences in growth rate can still have a big effect. For example, when encounter rate is 0.5·d^{-1}, only 0.047% of a cohort growing at 0.5 mm·d^{-1} would survive 60 d, but this is nearly 50-fold higher than the 0.001% survival a cohort growing at

0.3 $mm \cdot d^{-1}$ would experience. This difference could distinguish between a large year-class and recruitment failure.

Bloater recruitment in Lake Michigan seems to be dependent on the interaction of developmental and growth rates with predation. Individual bloaters which spend longer in the egg stage (due to colder temperatures for example) and larvae which are growing more slowly than others in their cohort are under-represented among the individuals that recruit (Rice et al. 1987b). Size-dependent predation interacting with variable growth rates among individuals could explain the bloater recruitment dynamics which we have observed. Of the predators encountered by bloaters during their early life history, sculpins in the hypolimnion and alewife in the epilimnion are most likely to be important to bloater recruitment. Any factor which reduces growth rate (e.g. low temperatures, low food) may lead to reduced recruitment if size-dependent sources of mortality such as predation are important. The strong negative relationship between alewife and bloater abundances likely results from both the direct impact of alewife preying on bloater larvae, and the indirect effects of resource competition prolonging the period in which larvae are most vulnerable to piscine predators.

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Mitochondrial DNA Variation among Anadromous Populations of Cisco (*Coregonus artedii*) as revealed by Restriction Analysis[1]

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Bernatchez, L., and J. J. Dodson. 1990. Mitochondrial DNA variation among anadromous populations of cisco (*Coregonus artedii*) as revealed by restriction analysis. Can. J. Fish. Aquat. Sci. 47: 533–543.

Mitochondrial DNA (mtDNA) restriction analyses were done to test the hypothesis that river populations of anadromous cisco from James-Hudson Bays that exhibit life-history variations are reproductively isolated. MtDNA variation among 141 cisco (*Coregonus artedii*) from eight rivers was studied with eight hexameric, four multihexameric and one multipentameric restriction enzymes which generated a mean of 78 fragments per fish. Pairwise sequence divergence estimates among the 19 mtDNA clones resolved were generally low but highly variable (mean: 0.52%, range: 0.08 to 1.03%). UPGMA and Wagner parsimony analysis revealed two major clonal groups which differed in diversity and geographic distribution; the more diversified (nucleon diversity index; 0.70) and less diversified (0.31) groups were twice as abundant in James and Hudson Bays, respectively. This suggests that cisco of James-Hudson Bays are derived from two glacial refugia and that they recolonized the area by two major postglacial routes. The frequency distribution analysis of all defined clones revealed significant stock discreteness among Hudson Bay populations and a lack of population subdivision in James Bay. The genetic structuring and diversity of anadromous cisco in James-Hudson Bay is discussed in relation to historical biogeographical events and to interactions of various life-history stages with the physical oceanographic environment.

Nous avons utilisé l'analyse de polymorphisme de longueur de fragments de restriction (PLFR) de l'ADN mitochondrial (ADNmt) pour tester l'hypothèse voulant que les populations de ciscos (*Coregonus artedii*) anadromes des baies James et d'Hudson démontrant des différences dans leur cycle vital soient isolées reproductivement. Nous avons étudié la variabilité de l'ADNmt de 141 ciscos provenant de huit rivières avec huit enzymes hexamériques, quatre multihexamériques et un multipentamérique qui ont généré en moyenne 78 fragments par poisson. L'estimé du pourcentage de divergence de séquence entre les 19 clones mitochondriaux identifiés était généralement faible mais très variable (moyenne: 0.52%, étendue: 0.08 à 1.03%). Les analyses de groupement selon l'association moyenne et de parcimonie de Wagner ont révélé deux groupes clonaux qui diffèrent par leur diversité et leur distribution géographique. Le plus diversifié (indice de diversité nucléique; 0.70) et le moins diversifié (0.31) de ces groupes étaient respectivement deux fois plus abondants dans la baie James et la baie d'Hudson. Ceci suggère que les ciscos des baies James et d'Hudson proviennent d'au moins deux refuges glaciaires et qu'ils ont recolonisé cette région par deux routes postglaciaires distinctes. L'analyse des fréquences de distribution de tous les clones identifiés a démontré que les populations de la baie d'Hudson mais non celles de la baie James étaient isolées reproductivement. Nous discutons l'hypothèse voulant que la structure et la diversité génétique des ciscos anadromes des baies James et d'Hudson soient déterminées par l'histoire biogéographique de l'espèce de même que par l'intéraction des différents stades de développement avec l'environnement océanographique physique du milieu.

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Anadromous populations of lake cisco (*Coregonus artedii*) inhabit large river systems of James and Hudson Bays. On the eastern coast, the species is found in variable abundance from the Rupert River to the Povungnituk River (Fig. 1) where it represents a major component of the domestic fisheries and a resource with potential for commercial exploitation by the native people (Morin and Dodson 1986). Knowledge of its population structure is thus becoming of major concern for adequate management and resource partitioning among native communities whose populations are expected to double within the next 25 yr.

Migration is an essential component at all stages of the life cycle of anadromous cisco (Dodson et al. 1986). In James Bay, the spring hatching period coincides with spring thaw, and larvae are flushed from the rivers into the bay. Juveniles and nonreproductive adults reenter the lower reaches of the rivers during the fall where they overwinter. The following spring, fish of all ages aggregate in the estuaries waiting for the retreat of the ice pack on the bay to migrate to feeding grounds. The upstream migration of mature fish begins by late summer and spawning occurs in late fall. Populations of Hudson Bay differ from those of James Bay by the absence of juvenile fish in the spring aggregation in estuaries which suggests that they either overwinter in different rivers or migrate early to the bay under the ice pack (Kemp et al. 1989).

Fish from different rivers exhibit differences in growth, age at maturity, reproductive effort, and mortality rate (Morin et al. 1982). These differences are believed to represent local adjust-

[1]Contribution to the program of GIROQ (Groupe Interuniversitaire de Recherches Océanographiques du Québec).

ments of the life history strategy resulting from trade-offs in energy allocation among growth, maintenance, and reproduction in response to different migration costs associated with the difficulty of upstream migration in each river. (Lambert and Dodson 1990; Kemp 1989). These differences fit the predictions of theoretical models of optimal reproductive strategies and thus fulfil the major criterion of local adaptation of the stock concept. However, the reproductive isolation of these populations remains to be demonstrated.

Morphological and ecological differences have been widely used to discriminate fish stocks (Ihssen et al. 1981). However, the problems in extrapolating phenotypic data to the underlying genotypic information are numerous (Ferris and Berg 1987). In the case of cisco species, the phentoypic variation observed among populations may be largely due to the influence of environmental factors during early development and thus cannot always provide strong evidence for reproductive isolation (Todd and Smith 1980; Todd et al. 1981). Because they are not environmentally influenced, genetic markers are more reliable than other traits for stock identification. Allozyme analysis has been widely used for this purpose and examples of its usefulness are numerous (Allendorf et al. 1986). However, this technique has failed to reveal differences between four species of Great Lakes ciscoes due primarily to a lack of allozyme polymorphism in this group of fish (Todd 1981).

In recent years, the analysis of mitochondrial DNA (mtDNA) polymorphism by restriction endonucleases has often been recognized as approaching the ideal method for quantifying genetic differences among populations (Avise 1987; Ferris and Berg 1987; Wilson et al. 1985). Two features of mtDNA enhance its utility for stock identification; its rapid evolution relative to the nuclear genome and its maternal mode of inheritance (Moritz et al. 1987). Currently used mtDNA analyses appear inadequate for the discrimination of mtDNA genotypes differing solely by the accumulation of mutations over the approximately 18 000 yr that have elapsed since the end of Wisconsinan glaciation (Wilson et al. 1985). However, stocks can be discriminated by the study of distribution frequencies of mtDNA polymorphisms that predate the genetic isolation of populations (Bentzen et al. 1989; Bernatchez and Dodson 1990; Bernatchez et al. 1989). Furthermore, the same mtDNA restriction analysis used for stock discrimination may provide insight into the historical biogeography of the species under study (Avise 1987).

In this paper, we report the results of mtDNA restriction analysis carried out to test the hypothesis that river populations of anadromous cisco from James-Hudson Bays are reproductively isolated. This study also provides a first database of mtDNA fragment size variability which will help orient sampling effort in studies of other populations of this species.

Methods

Sampling

Cisco from eight populations of the eastern coast of James-Hudson Bays were sampled at the mouth of their overwintering rivers during the spring of 1987 and at the end of the summer 1988 (Fig. 1; Table 1). In 1987, livers and developing ovaries were extracted from freshly caught specimens, frozen immediately and kept on dry-ice for several months before mtDNA was extracted. In 1988, mature ovaries were kept on wet ice and mtDNA was extracted within 10 d following capture.

Isolation and Restriction Enzyme Analysis of mtDNA

MtDNA was purified according to Gonzalez-Villa Señor et al. (1986) as modified by Bernatchez et al. (1988). MtDNA was digested separately with eight hexameric, four multihexameric and one multipentameric restriction endonucleases (Table 2). Mitochondrial DNA fragments were electrophoretically separated on 0.8 or 1.2% agarose gels for 16 h at 25 V.

Visualization of Restriction Fragments

When mtDNA was obtained in sufficient quality and quantity, ethidium bromide staining was sufficient to reveal the digested fragments. For many of the frozen samples with low or poor quality yield of mtDNA, DNA was denatured, neutralized, and transferred to nitrocellulose filters by the procedure described by Maniatis et al. (1982). Filters were hybridized with a highly purified radiolabeled total mtDNA probe. ^{32}P-labeled DNA with a specific activity of at least 10^8 cpm/μg was prepared with ^{32}P-dATP and ^{32}P-dCTP. The nick translation reaction contained 2 μL of highly purified mtDNA (40–80 ng·μL^{-1}), 2.5 μL of 10× NT buffer (Maniatis et al. 1982), 1 μL of each unlabelled dGTP and dTTP (1 μmol·μL^{-1}), 5 μL of each labeled ^{32}P-dATP and ^{32}P-dCTP (29.6 TBq = 800 Ci·mmol^{-1}), 2.0 μL of EDTA (1 mM) and 1.0 μL of DNase (10 ng·μL^{-1}). Distilled water was added to a final volume of 25 μL. The reaction was left 10 min at room temperature, then 1 μL of DNA polymerase 1 (10·μL^{-1}) was added to the mixture and left 45 min at room temperature. The reaction was stopped with 500 mM EDTA to a final concentration of 20 mM and the volume adjusted to 40 μL with 1× TE buffer (Maniatis et al. 1982). The nick-translated DNA was then separated from unincorporated nucleotides by column chromatography on Sephadex G-100 medium (Maniatis et al. 1982). The nitrocellulose filters were prehybridized and hybridized individually in a plastic bag following the procedures of Wahl et al. (1979). Filters were autoradiographed using an intensifying screen (Cronix lightning-plus) for 2 to 16 h.

Data Analysis

Size estimates of fragments were made by running simultaneously into the agarose gel digests of phage lambda DNA with *Hind*III and *Eco*RI-*Hind*III double digest. No attempt to score fragments less than 350 base pairs was made. Distinct single endonuclease patterns were identified by a specific letter in order of appearance. Each fish was assigned a multi-letter code which described its composite mtDNA genotype.

Sequence divergence between genotypes was estimated according to Upholt's (1977) fragment method. Sequence divergence and standard deviation were estimated independently for hexameric and multihexameric enzymes (*Ava*II was treated with multihexameric) and both estimates were then pooled following weighting for the number of base pairs sampled by each type of enzyme. The resulting distance matrix was clustered by UPGMA (Sneath and Sokal 1973) using the average linkage algorithm of the SAS statistical package. The diversity of mtDNA lineages was estimated with Nei and Tajima's (1981) nucleon diversity index;

$$h = \frac{1}{n-1}\left[n\left(1 - \sum_{i=1}^{l} x_i^2\right)\right],$$

where x_i is the frequency of the ith type of mtDNA in a population of n specimens and l is the number of mtDNA types.

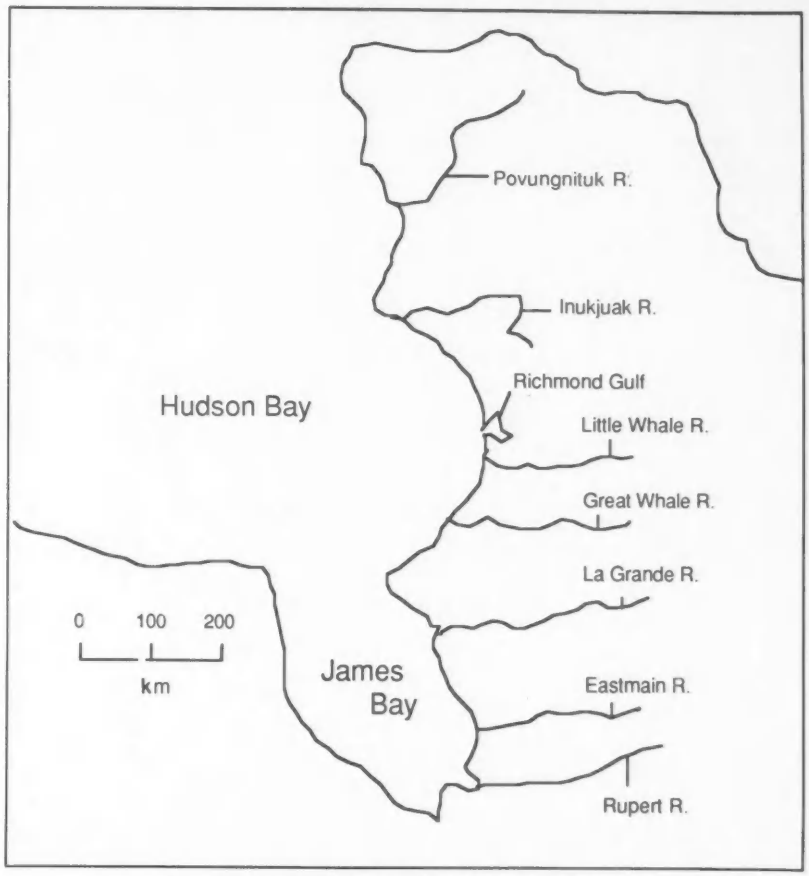

FIG. 1. Location map with sampling sites of anadromous cisco.

TABLE 1. Sample locations, sample sizes, number of clonal lines, and estimated nucleon diversity for anadromous cisco populations sampled in James-Hudson Bays. Nucleon diversity was not estimated for the Great Whale and Inukjuak because of small sample sizes.

Population	Sample size	Genotypes number	Nucleon diversity
James Bay			
Rupert River	22	9	0.83
Eastmain River	29	9	0.85
La Grande River	27	8	0.83
Hudson Bay			
Little Whale River	17	4	0.55
Richmond Gulf	17	2	0.52
Povungnituk River	19	4	0.71
Great Whale River	4	3	—
Inukjuak River	6	4	—

The mtDNA clones were organized into a Wagner network using the Metro algorithm of the Phylip package provided by Joe Felsenstein (Department of Genetics, University of Washington, Seattle, WA 98195).

The geographical heterogeneity in the frequency of mtDNA genotypes among populations was analyzed using the randomized generation of chi-square distribution by a Monte Carlo technique (Roff and Bentzen 1989). This procedure circumvents the problem of low sample size by estimating the probability of obtaining a chi-square value larger than that observed by randomization of the original data sets. By this method, the accuracy of the estimate of Type 1 error depends only upon the number of randomizations of the original data sets. In this case, 1000 randomizations were performed.

We also estimated the likelihood of detecting mitochondrial DNA diversity at the population and regional levels within the confines of our sampling protocol. To do so, we adopted the combinatorial approach of Hebert et al. (1988). The relationship between the number of clones detected as a function of sample size was estimated by an incremental random choice of individuals. This procedure was done at the population level and also at the regional level by pooling all fish from a given region. An increment choice of three fish at the population level and five fish at the regional level was used to estimate the number of clones detected for each incremental step. The procedure was repeated 10 times for each sampling intensity to generate an estimate of random sampling variance. The relationship between the number of clones detected as a function of genome

TABLE 2. Fragment size estimates (base pairs) for all fragment patterns resulting from the restriction analysis of cisco mtDNA. No attempt to estimate fragments below 350 base pairs was made.

*Ava*I					*Ava*II					*Ban*I	
A	B	C	D	E	A	B	C	D	E	A	B
3 550	3 550	3 740	3 550	3 550	4 800	4 800	4 800	4 800	4 800	3 700	3 700
2 950	2 950	3 550	2 950	2 950	1 675	1 675	1 675	1 675	2 160	2 550	2 550
2 500	2 650	2 500	2 500	2 500	1 450	1 450	1 450	1 450	1 675	2 200	2 200
2 400	2 500	2 400	2 500	2 400	1 300	1 300	1 425	1 425	1 450	2 000	2 000
1 550	1 550	1 550	1 550	1 550	1 250	1 250	1 300	1 300	1 300	1 700	1 575
1 250	1 250	1 250	1 250	1 250	970	970	970	1 075	970	1 150	1 150
1 150	1 150	1 150	1 150	1 150	910	970	910	970	770	880	880
850	850	850	850	790	770	770	770	770	750	800	800
790	790		790	620	750	750	750	750	450	740	740
					450	450	450	450	450	380	380
					450	450	450	450	360		
					360	360	360	360	350		
					350	350	350	350			
16 990	17 140	16 990	17 090	16 760	15 485	15 545	15 660	15 825	15 485	16 100	15 975

*Dra*I		*Hae*II						*Hinc*II				*Pvu*II
A	B	A	B	C	D	E	F	A	B	C	D	
5 600	6 150	4 300	4 300	4 850	4 300	4 300	4 850	6 400	6 400	6 400	6 400	9 500
4 600	4 600	4 300	4 300	4 300	3 900	4 300	4 300	2 900	2 900	2 150	2 900	5 000
3 300	3 300	3 700	3 700	3 700	3 700	3 700	3 700	2 050	2 050	2 050	2 050	1 640
1 625	1 625	1 400	1 400	1 400	1 400	1 400	1 400	1 575	1 750	1 575	1 700	860
690	690	1 100	1 200	1 100	1 100	1 100	1 100	1 450	1 575	1 450	1 450	
630	630	920	1 100	920	920	1 000	1 100	1 125	1 125	1 125	1 125	
550		825	825	825	825	825	825	840	840	840	840	
		550	550		550	550				750		
					400							
16 995	16 995	17 095	17 375	17 095	17 095	17 175	17 275	16 340	16 640	16 340	16 465	17 000

*Bgl*I		*Hind*III			*Sma*I	*Xmn*I			*Bam*HI	*Pst*II	
A	B	A	B	C		A	B	C		A	B
8 100	7 600	4 220	4 220	4 220	9 400	7 600	5 050	7 600	17 000	11 780	11 780
7 600	7 600	3 500	3 800	3 740	7 550	5 050	5 050	5 050		2 700	4 750
1 300	1 300	3 500	3 500	3 500		4 200	4 200	2 850		2 050	470
	500	3 200	3 200	3 200			2 550	1 350		470	
		2 400	2 400	2 400							
17 000	17 000	16 820	17 120	17 060	16 950	16 850	16 850	16 850	17 000	17 000	17 000

sampling intensity was estimated by incremental random choice of restriction enzymes. Results were obtained by an incremental choice of two restriction enzymes at both population and regional levels. The random choice of enzymes was repeated 10 times for each incremental step. As different restriction enzymes produced different numbers of fragments, we attributed the fragment numbers to their respective restriction enzymes which yielded a sum of the fragments for any enzyme combination.

Results

Restriction Sites Variation

The 13 enzymes used generated a total of 105 restriction fragments with a mean of 78 per individual. Considerable polymorphism was observed among the 141 cisco analyzed. All enzymes but three were polymorphic (Table 2) which allowed identification of 19 mitochondrial genotypes (Table 3). The estimated nucleon diversity among all fish analyzed was 0.79. This value is intermediate within the values calculated for other fish species that were studied over a wide geographic range using similar analyses (Table 4). The mean size of mtDNA genome as estimated by averaging the sums of all digestion patterns but *Ava*II (omitted because of the number of undetected small fragments) was 16 945 bp ± 240 (SD). The length estimate for the mtDNA molecule of *C. artedii* falls within the values observed in other fishes studied to date (data compiled in Billington and Hebert 1988; Kornfield and Bogdanowicz 1987; Bentzen et al. 1989). Pairwise sequence divergence estimate between all mtDNA clones was generally low but highly variable (mean: 0.52 ± 0.22 (SD), range: 0.08 to 1.03%) (Table 5). Clustering of the distance matrix by UPGMA revealed two major clonal groups (A, B) separated by a mean sequence divergence of 0.52% (Fig. 2). These composed respectively 50 and 45% of the 141 fish analyzed. The remaining 5% was distributed among five highly divergent clones (group C). The Wagner parsimony analysis generated a total of 31 equally parsimonious networks requiring a minimum

TABLE 3. Description of clonal lines, number of individual fish, and frequency distribution of each clone observed among anadromous cisco from James-Hudson Bays. Composites represent the following order of enzymes; *Ava*I, *Ava*II, *Ban*I, *Bg*1I, *Dra*I, *Hae*II, *Hinc*II, *Hind*III, *Pvu*II, *Sma*I, *Xmn*I, *Pst*I, *Bam*HI.

Clone	Composite	No. of fish	James Bay			Hudson Bay				
			Rupert	Eastmain	LaGrande	Great Whale	Little Whale	Richmond Gulf	Inukjuak	Povungnituk
1	A A A A A A A A A A A A A A	53	7	6	8	1	11	10	1	9
2	A A A A A A A A A A A A A B	1					1			
3	A A A A A A A B A A A A A A	1				1				
4	A A A A A A A C A A A A A A	1	1							
5	A A A A A D A A A A A A A A	2	1						1	
6	A A A A B A A A A A A A A A	4								4
7	A C A B A C A A A A A A A A	1	1							
8	A C B B A A A A A A A A A A	33	6	8	4		4	7	2	2
9	A C B B A A A A A A B A A A	1		1						
10	A C B B A A A A A A C A A A	15	1	6	7		1			
11	A C B B A A C A A A A A A A	8	3	2	3					
12	A C B B A C A A A A A A A A	11	1	3	1				2	4
13	B B B B B B A A A A A A A A	1				1				
14	C C B B A C A A A A A A A A	1			1					
15	D B A A A E B A A A A A A A	1				1				
16	D D B B A C D C A A A A A A	2			2					
17	D D B B A F D C A A A A A A	2	1	1						
18	D E B B A E B A A A A A A A	1		1						
19	E A A A A A A A A A A A A A	2		1	1					

TABLE 4. mtDNA nucleon diversity index estimated for various species studied by conventional restriction analysis in a wide geographic range. Maximum possible value is 1.0. Only studies covering a wide geographic distribution of the species and performed with a comparable number of restriction enzymes were selected to reduce sampling biases. However, these values should be considered with caution as different enzymes were used in different studies.

Species	Diversity	Reference
Atlantic menhaden *(Brevoortia tyrannus)*	0.99	Avise et al. 1989
Warmouth sunfish *(Lepomis gulosus)*	0.97	Bermingham and Avise 1986
European whitefish *(Coregonus lavaretus)*	0.95	Bernatchez et al. 1989
Atlantic herring *(Clupea harengus)*	0.91	Kornfield and Bogdanowicz 1987
Pacific herring *(C. harengus pallasi)*	0.91	Schweigert and Withler 1990
Bowfin *(Amia calva)*	0.81	Bermingham and Avise 1986
Cisco *(Coregonus artedii)*	0.79	Present study
American shad *(Alosa sapidissima)*	0.79	Bentzen et al. 1989
Lake trout *(Salvelinus namaycush)*	0.77	Grewe and Hebert 1988
Brown trout *(Salmo trutta)*	0.72	Gyllensten and Wilson 1986
Redear sunfish *(Lepomis microlophus)*	0.68	Bermingham and Avise 1986
Chinook salmon *(Oncorhynchus tshawytscha)*	0.60	Wilson et al. 1987
Walleye *(Stizostedion vitreum)*	0.55	Billington and Hebert 1988
American eel *(Anguilla rostrata)*	0.54	Avise et al. 1986
Hardhead catfish *(Arius felis)*	0.47	Avise et al. 1987b
Lake whitefish *(Coregonus clupeaformis)*	0.31	Bernatchez et al. 1989

of 35 site changes. Figure 3 illustrates the mutational steps required to move from one clone to another. Clone 8 (group B) appeared central in the minimum number of steps required to move to any clonal line. It was never more than eight steps distant from any clone while the maximum number of steps required between two clones was 15 (clones 13 and 17). Clonal group A and B were separated by one *Ban*I and *Bgl*I site gain and two *Ava*II site losses. Clonal lines pooled into group C in UPGMA differed from one another and from group A and B by many site gains or losses. Other trees obtained differed from Fig. 3 mainly by alternative positions and mutational steps related to these clonal lines.

Geographic Variation

A significant difference in the frequency distribution of clonal groups A and B was observed among populations (Table 6). It is apparent that this heterogeneity is due to a genetic split between James and Hudson Bays. Clonal group A was most abundant in populations of Hudson Bay while clonal group B was most abundant in populations of James Bay (Fig. 4). The overall ratio of A/B was 1.94 in Hudson Bay compared with 0.52 in James Bay. James Bay also differed by the presence of group C clones in all populations as opposed to their absence in Hudson Bay. Clonal group B exhibited a much higher nucleon diversity index (0.70) than A (0.31). Thus, the estimated diversity index was higher for any population of James Bay than Hudson Bay (Table 1).

The frequency distribution analysis of all defined clones revealed no evidence of stock discrimination among James Bay populations ($\chi^2 = 25.49$, df = 6, $P > 0.25$, 506/1000 random-

TABLE 5. Pairwise percent sequence divergence estimates (below diagonal) with corresponding standard deviation (above diagonal) calculated for clonal lines observed among anadromous cisco from James-Hudson Bays. This distance matrix was used to cluster clonal lines by UPGMA.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	0	0.12	0.15	0.15	0.18	0.18	0.2	0.2	0.23	0.17	0.22	0.23	0.28	0.25	0.27	0.27	0.29	0.24	0.18
2	0.13		0.13	0.13	0.18	0.13	0.24	0.24	0.26	0.21	0.26	0.27	0.3	0.29	0.21	0.3	0.33	0.28	0.18
3	0.09	0.23		0.15	0.16	0.24	0.23	0.22	0.24	0.18	0.25	0.26	0.29	0.28	0.2	0.27	0.29	0.28	0.16
4	0.09	0.23	0.09		0.16	0.24	0.23	0.22	0.24	0.18	0.25	0.26	0.29	0.28	0.2	0.24	0.26	0.28	0.16
5	0.13	0.26	0.21	0.21		0.18	0.21	0.23	0.26	0.23	0.24	0.23	0.3	0.25	0.32	0.27	0.3	0.25	0.25
6	0.14	0.28	0.24	0.24	0.26		0.24	0.23	0.25	0.18	0.26	0.27	0.24	0.29	0.22	0.3	0.33	0.29	0.18
7	0.35	0.49	0.44	0.44	0.39	0.5		0.25	0.21	0.17	0.29	0.18	0.26	0.25	0.25	0.17	0.21	0.39	0.23
8	0.34	0.48	0.44	0.44	0.48	0.49	0.27		0.17	0.17	0.14	0.17	0.23	0.25	0.25	0.21	0.21	0.29	0.23
9	0.48	0.63	0.59	0.59	0.61	0.65	0.38	0.13		0.19	0.15	0.17	0.26	0.21	0.29	0.27	0.26	0.22	0.26
10	0.36	0.51	0.47	0.47	0.48	0.53	0.26	0.25	0.39		0.2	0.21	0.29	0.23	0.27	0.25	0.28	0.24	0.23
11	0.43	0.57	0.52	0.52	0.57	0.58	0.36	0.08	0.21	0.34		0.23	0.24	0.29	0.25	0.22	0.21	0.32	0.34
12	0.48	0.63	0.57	0.57	0.53	0.63	0.13	0.13	0.25	0.38	0.22		0.24	0.18	0.26	0.2	0.19	0.34	0.24
13	0.67	0.82	0.77	0.77	0.81	0.54	0.79	0.48	0.61	0.75	0.57	0.63		0.26	0.27	0.29	0.28	0.23	0.3
14	0.64	0.78	0.72	0.72	0.68	0.78	0.27	0.27	0.38	0.53	0.36	0.13	0.79		0.27	0.21	0.21	0.39	0.26
15	0.32	0.45	0.39	0.39	0.46	0.44	0.68	0.67	0.8	0.66	0.78	0.84	0.62	1.02		0.27	0.29	0.21	0.32
16	0.63	0.78	0.63	0.54	0.67	0.78	0.26	0.54	0.66	0.52	0.64	0.39	0.87	0.55	0.67		0.23	0.22	0.28
17	0.87	1.02	0.87	0.79	0.92	1.02	0.49	0.48	0.61	0.76	0.58	0.35	0.71	0.49	0.81	0.22		0.21	0.31
18	0.63	0.77	0.71	0.71	0.78	0.76	0.68	0.36	0.47	0.62	0.45	0.51	0.48	0.68	0.39	0.64	0.48		0.25
19	0.13	0.26	0.21	0.21	0.27	0.26	0.48	0.48	0.61	0.48	0.57	0.63	0.81	0.79	0.46	0.77	1.03	0.78	0

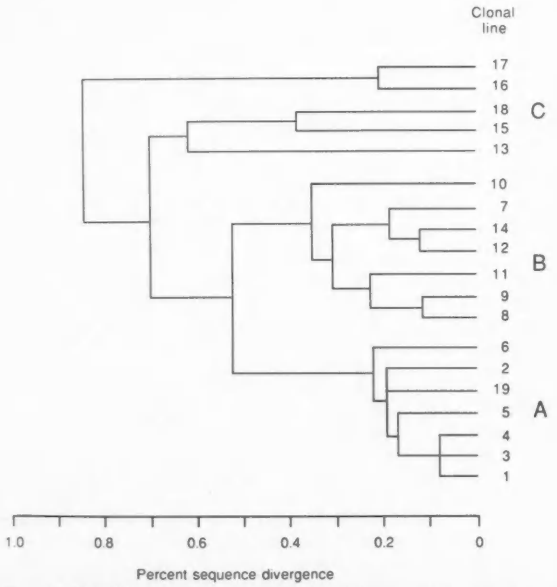

FIG. 2. UPGMA phenogram clustering the distance matrix of sequence divergence between anadromous cisco clonal lines.

ized $\chi^2 > \chi^2$ observed). In Hudson Bay, the Povungnituk River population clearly differed from the homogeneous assemblage of Little Whale River and Richmond Gulf populations ($\chi^2 = 18.24$, df = 5, $P < 0.005$, 0/1000 randomized $\chi^2 > \chi^2$ observed). The Little Whale River - Richmond Gulf assemblage also differed significantly from James Bay ($\chi^2 = 25.62$, df = 14, $P < 0.05$, 11/1000 randomized $\chi^2 > \chi^2$ observed). Although not statistically demonstrated, further structuring in Hudson Bay is suggested by the addition of Great Whale and Inukjuak Rivers. For example, three unique clonal lines were found among four fish sampled in the Great Whale River (Table 3).

Sampling and Detection of mtDNA Diversity

The number of mtDNA clones detected as a function of number of individuals or restriction fragments samples was always higher in James Bay. At the population level, the number of genotypes increased smoothly with the number of fish sampled and approached an asymptotic value of close to nine with a sample of 21 fish in James Bay compared with a value of three with a sample of 15 fish in Hudson Bay (Fig. 5). This suggests that 21 and 15 specimens were sufficient to detect all variability within a given population of James and Hudson Bay, respectively. The same relationship did not tend towards an asymptotic value at the regional level which demonstrates that detection of all mitochondrial variability in both regions would require higher sample sizes (Fig. 5).

The number of genotypes detected at the population level increased with the number of restriction fragments sampled and reached an asymptotic value of close to three with a sample of about 50 fragments in Hudson Bay (Fig. 6). In James Bay, however, a sample of 78 fragments was still insufficient to detect all mtDNA variants. This conclusion also applied at the regional level in both James and Hudson Bay.

Discussion

Mitochondrial DNA Variation and Postglacial Colonization

It has been suggested that contemporary observations of intraspecific genetic structure and diversity have been determined to a large degree by historical geographic factors (Avise et al. 1987a; Bermingham and Avise 1986). The extent to which the Wisconsinan glaciation may have influenced the structure and diversity of cisco populations of James-Hudson Bays is illustrated by a comparison of the nucleon diversity index observed for anadromous populations of cisco with those of lake whitefish (*C. clupeaformis*) and European whitefish (*C. lavaretus*). Lake whitefish from James-Hudson Bays exhibit the lowest nucleon diversity reported in the literature while European whitefish from the Baltic Sea have one of the highest (Table 4), despite similar life cycles and close phylogenetic relationships. We have previously argued that this difference

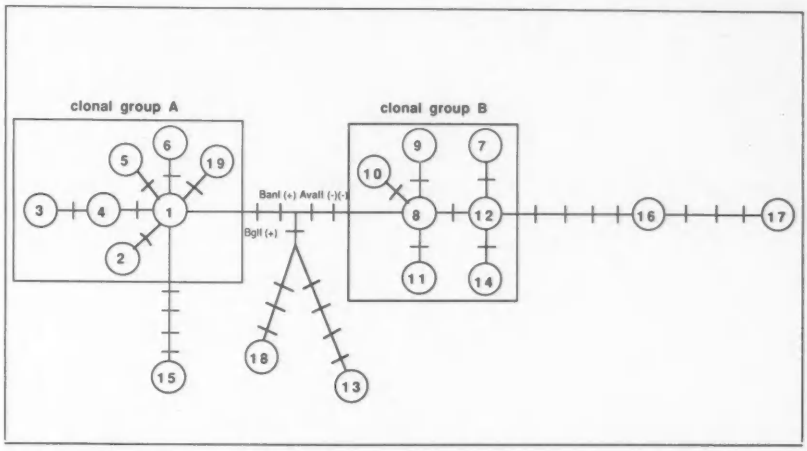

FIG. 3. Parsimony network linking the 19 cisco mtDNA clones revealed by restriction analysis. Clonal groups A and B refer to clusters identified by UPGMA. Site gains (+) or losses (−) that differentiate the two clonal groups are indicated. Sites differences were inferred from differences in fragment patterns among clonal lines.

TABLE 6. Chi-square analysis of the observed frequency distribution of clonal groups A and B among anadromous populations of cisco in James-Hudson Bays. Expected frequencies are given in brackets. $X^2 = 14.35$, df = 5 $P < 0.05$.

	Populations					
	James Bay			Hudson Bay		
Clonal group	Rupert	Eastmain	LaGrande	Little Whale	Richmond Gulf	Povungnituk
A	9(10)	7(12.9)	9(11.9)	12(8.1)	10(8.1)	13(9.1)
B	12(11)	20(14.1)	16(13.1)	5(8.9)	7(8.9)	6(9.9)

may be due to the greater extent of the ice sheet in North America compared with Eurasia during the last glaciation events that led to a more intense bottleneck effect for lake whitefish thus reducing mtDNA variability (Bernatchez et al. 1989). However, cisco from James-Hudson Bays exhibit a nucleon diversity more than twice that of lake whitefish from the same area, and consequently other factors must be considered to explain such differences.

A major genetic difference between the two species in James-Hudson Bays is the existence of two major divergent mtDNA clusters revealed in *C. artedii* as opposed to only one for *C. clupeaformis*. In addition, highly divergent lineages were observed in *C. artedii*. Avise et al. (1984) demonstrated that mtDNA variability observed today is largely influenced by stochastic lineage extinction which in turn is a function of time since population founding, generation time, density regulation, long term effective population size, and population subdivision. The first three parameters are quite similar for these two species such that they are unlikely to have led to dissimilar stochastic lineage extinction. A possible hypothesis is that numerous highly distinct lineages were retained in *C. artedii* because of a much higher abundance of the ancestral population that recolonized James-Hudson Bays. However, while the sorting and subsequent coexistence of highly divergent lineages within a single large population lacking geographic subdivision is theoretically possible, such a situation has not been observed in any species assayed to date (Avise et al. 1988).

An alternative and more plausible hypothesis is that historical population subdivisions in *C. artedii* led to retention of divergent lineages in different refugia. Such population subdivisions provide a buffering effect against lineage extinction (Avise et al. 1984). Hence, although the diversity of lineages within each isolated population was low, the overall diversity within the species could remain high. For example, Billington and Hebert (1988) observed two major mtDNA clonal groups among walleye (*Stizostedion vitreum*) which they associated with different glacial refugia. Nucleon diversity indices calculated independently for each group were low (0.16 and 0.18) but the overall estimate remained relatively high (0.55). In the case of *C. artedii*, it is possible that the two major mtDNA clusters A and B identify ancient populations that evolved in two separate glacial refugia which subsequently recolonized James-Hudson Bays following the retreat of the ice sheet. Fish from only one refugium would have recolonized this area in the case of *C. clupeaformis*. The analogy in overall diversity observed between *C. clupeaformis* (0.31) and cluster A of *C. artedii* (0.31) suggests these two groups of fish may have survived in the same refugium and have undergone similar bottleneck effects during the last glaciation.

Further evidence that clonal groups A and B are derived from two different refugia is provided by their different geographic distributions. Cluster A is twice as abundant as cluster B in populations of Hudson Bay, whereas the reverse is true in James Bay (Fig. 4). Crossman and MacAllister (1985) argued that

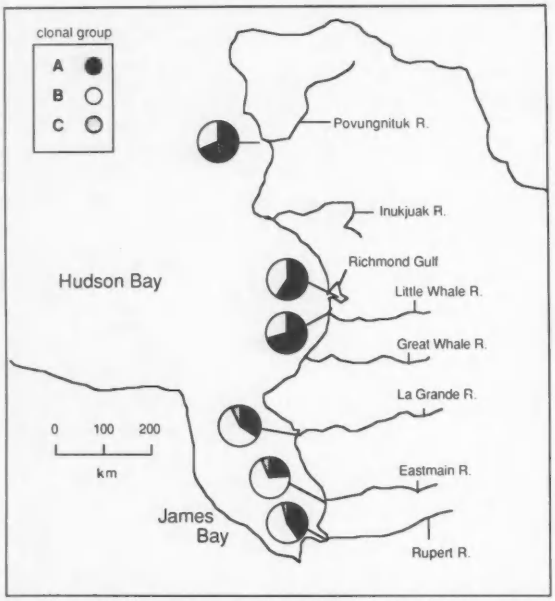

FIG. 4. Distribution of the A (black), B (white), and C (dotted) mtDNA clonal groups identified by UPGMA.

recolonization of the modern Hudson Bay system was possible by two major routes. The earliest connection was via the northwest coast of Hudson Bay followed later by the opening of southern James Bay. Therefore, one group of cisco (clonal group A) may have recolonized the area from the north and the other (clonal group B) from the south. Mixing of the two lineages has occurred since then without completely overriding the historical geographic influences on population subdivision. The genetic evidence for the existence of two major glacial refugia was also noted in lake trout (*Salvelinus namaycush*) and walleye (Grewe and Hebert 1988; Billington and Hebert 1988). Both these studies revealed two major mtDNA clonal groups among fish from the Great Lakes area that the authors associated with recolonization of the area from different refugia. Such concordant gene pool fragmentation among independently evolving species may indicate influences of a shared biogeographic history and suggest the existence of generalized tracks for these species (McDowall 1978).

The presence of five highly divergent clonal lines (cluster C) in James Bay also contributes to the higher nucleon diversity observed for *C. artedii* as opposed to *C. clupeaformis*. However, their origin is problematic as they diverge highly either from clonal group A or B and among themselves. It is possible that they represent introgressed mtDNA of other cisco species, but this hypothesis remains to be tested.

Geographic Variation of mtDNA Lineages

Based on life history variations, it was tacitly accepted that river populations of anadromous cisco in James-Hudson Bays are reproductively isolated. Thus, the premise of this study was that mtDNA restriction analysis should have differentiated each of them. While no unique population specific markers were found, statistical differences in the frequency distribution of mtDNA clones demonstrate that cisco spawning in particular river systems form discrete reproductive units. Three distinct genetic pools were identified; (1) Povungnituk River, (2) Richmond Gulf-Little Whale River, and (3) all James Bay rivers. Further structuring in Hudson Bay is also suggested by the clonal lines distribution in Great Whale and Inukjuak Rivers. Results obtained for Hudson Bay contrast with the absence of population subdivisions revealed in James Bay. Several reasons could explain the apparent low population structuring in James Bay; (1) the stochastic effect of low sample size, (2) genotypes common to all populations are ancestral mtDNAs which remained widespread following the genetic isolation of populations, and (3) the homogeneity of mtDNA lineage distribution reflects ongoing gene flow among river populations. The first two explanations cannot be strictly ruled out. However, it is hardly conceivable that these two phenomena would prevent stock discrimination only among populations of James Bay and not those from Hudson Bay. For instance, sample sizes were even smaller in Hudson Bay and yet allowed stock discrimination.

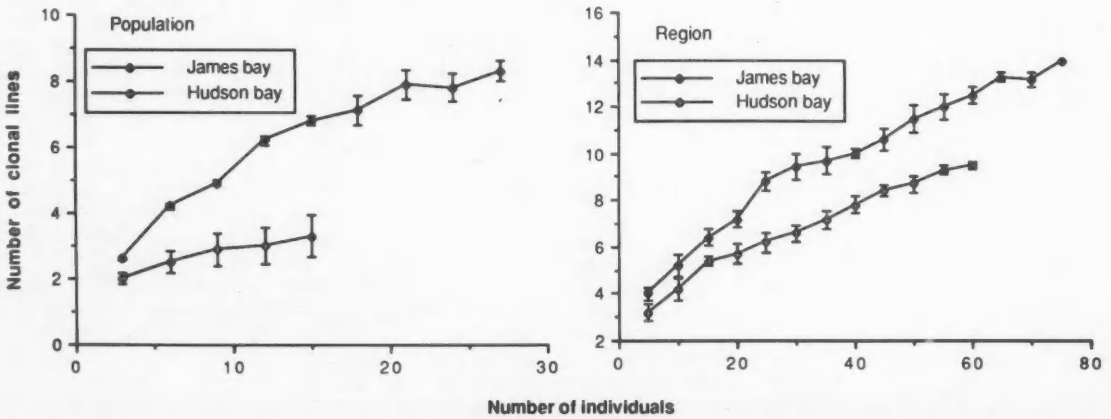

FIG. 5. Effect of fish sample size on the number of mtDNA clonal lines detected within populations and within each the James Bay region and the Hudson Bay region. Results were obtained by an incremental random choice of three fish at the population level and of five fish at the regional level. The procedure was repeated 10 times for each incremental step. Standard error is indicated by vertical bar.

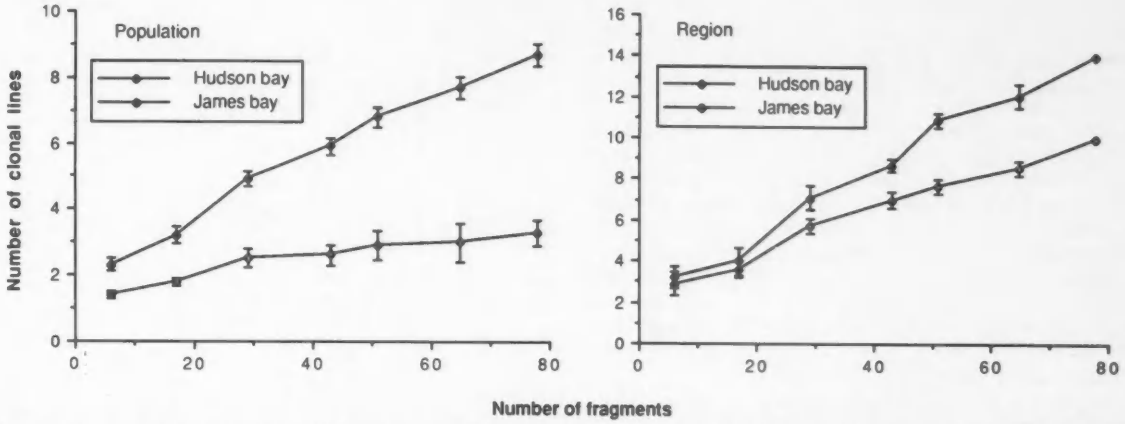

FIG. 6. Effect of the resolution of mtDNA restriction analysis on the number of clonal lines detected within populations and within regions (James Bay and Hudson Bay). Results were obtained by an incremental random choice of two restriction enzymes. Number of enzymes were then converted into the corresponding number of fragments analysed for each incremental step. The procedure was repeated 10 times for each incremental step. Standard error is indicated by vertical bars.

We propose that the absence of population structure in James Bay is the result of gene flow among rivers. There is considerable evidence that the population structure of many fish species is defined during the early life history stages. Two factors are essential for maintaining population integrity; (1) the existence of well defined physical oceanographic or geographic features in which larvae maintain themselves through behavioral and passive mechanisms, and (2) the homing capacity of the adult fish to spawning grounds (Sinclair and Iles 1988). Evidence of homing to natal sites in coregonid fishes is provided by tagging experiments but the degree of precision in this behaviour is not documented. In the case of anadromous cisco from James Bay, tagging experiments did not reveal homing but instead demonstrated straying among rivers (Lambert and Dodson 1982). For instance, four out of six recaptured fish tagged in the Eastmain River were caught in three rivers located between 50 and 170 km from the tagging site. In addition, the study of larval movements suggests that larvae are not retained within each river or estuary. Ochman and Dodson (1982) found that coregonine larvae from the Eastmain River are flushed out of the river and transported passively into the bay soon after hatching. This appears to represent a mechanism to exploit the greater availability of food in the Bay. A major oceanographic feature of James Bay is the existence of a cyclonic gyre during the summer months (Prinsenberg 1986). In this system, cold and highly saline Arctic water masses from Hudson Bay enter along the western shore of James Bay, are heated and diluted as they progress southward, resulting in a cyclonic current of warmer and brackish water (as low as 10 $g \cdot kg^{-1}$) which can reach speeds of up to 19 $cm \cdot s^{-1}$ on the northeastern coast of James Bay. It is likely that cisco larvae flushed into the Bay may be trapped in this gyre. In such a case, all of James Bay would act as a geographic retention zone. This, along with an apparent imprecision of adult homing, is consistent with the hypothesis that cisco from all James Bay rivers represent a unique gene pool. An analogous situation in which fish do not home to specific natal rivers but to a wide geographic area of retention has been documented for the rainbow smelt (*Osmerus mordax*) in the Gulf of St. Lawrence (Fréchet et al. 1983; Ouellet and Dodson 1985).

The same potential for gene flow also exists in Hudson Bay but its realization may be hampered by ecological barriers. A cyclonic pattern of circulation analogous to James Bay also exists in Hudson Bay (Prinsenberg 1986) in which larval cisco could be trapped. However, the waters of the two systems differ in respect to many physico-chemical characteristics. Unlike James Bay, Hudson Bay is more typically oceanic and high salinity (>24 $g \cdot kg^{-1}$) is found all along the coast, except in the plumes of major rivers. The high salinity encountered in Hudson Bay may prevent transport of larval cisco over long distances. Studies of salinity tolerance of larvae of anadromous populations of two species of cisco, *C. albula* and *C. sardinella* revealed a maximum salinity tolerance between 8 and 13 $g \cdot kg^{-1}$ for the two species (Girsa et al. 1980; Jager et al. 1981). If *C. artedii* exhibits a similar salinity tolerance, larval cisco trapped in the gyre of Hudson Bay and transported away from river plumes would not survive. This would limit gene flow along the coast and river populations would be maintained mainly by larvae remaining in the estuary of each river, resulting in population subdivision.

Management Implications

The basic premise of fish stock conservation and sustainable harvesting is that each stock should be managed separately (MacClean and Evans 1981). This study revealed at least two separate reproductive units of *C. artedii* in Hudson Bay and suggests that there may be more structuring. Therefore, it is advisable that each river system of Hudson Bay should be managed individually, except for the homogeneous Little Whale–Richmond Gulf complex. Results for James Bay do not support the stock hypothesis. Nevertheless, caution must be taken in concluding that no stock structure exists as the absence of genetic differences among populations does not allow us to categorically conclude that there is gene flow among rivers. Based on the number of clonal lines detected as a function of restriction enzymes (Fig. 6), it is clear that more variability would have been detected by increasing the number of enzymes used. Although it is theoretically possible that a more comprehensive analysis may reveal population structuring, the absence of pop-

ulation subdivision is corroborated by the apparent absence of larval retention in each river and by the demonstration of straying among rivers in tagging experiments. We thus conclude that it is advisable to consider the eastern coast of James Bay as a management unit.

Mitochondrial DNA restriction analysis allowed us to identify distinct genetic pools among anadromous *C. artedii* of James-Hudson Bay. Thus, our results support the genetic model of life history variations observed among anadromous cisco populations of Hudson Bay and between populations from James and Hudson Bay. On the other hand, the lack of genetic substructuring observed in James Bay suggests that reproductive isolation is not a prerequisite for life history variation.

In conclusion, the genetic structuring of anadromous cisco in James-Hudson Bay appears to be determined by historical biogeographical events and by the interaction of the various life-history stages with the physical oceanographic environment of the area.

Acknowledgments

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Pharmacokinetics and Tissue Disposition of the Off-Flavor Compound 2-Methylisoborneol in the Channel Catfish (*Ictalurus punctatus*)[1]

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The tissue disposition of the off-flavor compound 2-methylisoborneol (MIB) was examined in market-sized channel catfish (*Ictalurus punctatus*). Purified MIB was intravascularly administered to channel catfish at a dosage of 1 $mg \cdot kg^{-1}$ body weight. Body tissues and fluids were collected at intervals following administration and were analyzed for MIB by microwave distillation and capillary gas chromatography. Plasma clearance of MIB was characterized by a two-compartment open model with half-lives of 0.14 and 3.62 h for distribution and elimination phases, respectively. MIB was more concentrated in peritoneal fat and subepidermal adipose tissue than in other tissues. The concentration in the edible flesh decreased from 0.107 $\mu g \cdot g^{-1}$ at 2 h to 0.025 $\mu g \cdot g^{-1}$ at 96 h. There was no evidence of biotransformation of MIB to the related compounds 2-methylenebornane and 2-methyl-2-bornene over the 96-h sampling period. The low recoveries of the administered dose in body fluids and tissues and the rapid clearance suggested significant gill excretion of this compound.

Le dépôt dans les tissus du 2-méthylisobornéol (MIB), un composé à la flaveur atypique, a été étudié chez des barbues de rivière de taille commerciale (*Ictalurus punctatus*). Le MBI purifié a été injecté par voie intra-veineuse à des barbues de rivière en dose de 1 $mg \cdot kg^{-1}$. Les tissus et les fluides ont été prélevés à différents intervalles après les injections et la concentration en MIB a été dosée par distillation à hyperfréquences et par chromatographie capillaire en phase gazeuse. La clearance plasmatique du MIB a été caractérisée par un modèle ouvert à deux compartiments à une demi-vie de 0,14 et 3,62 h, pour la phase de distribution et la phase de l'élimination, respectivement. Le MIB s'est davantage concentré dans le tissu adipeux péritonéal et subépidermique. La concentration dans les chairs comestibles est passée de 0,107 $\mu g \cdot g^{-1}$, aprés 2 h, à 0,025 $\mu g \cdot g^{-1}$, après 96 h. Rien n'indique qu'il se soit produit une biotransformation du MIB dans ses composés apparentés, le 2-méthylènebornane et le 2-méthyl-2-bornène, au cours des 96 h d'échantillonnage. Le faible taux de récupération du MIB injecté dans les fluides et les tissus corporels ainsi que la clearance rapide indiqueraient qu'il se produit une excrétion importante de ce composé par les branchies.

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The contamination of water with compounds of objectional taste and odor (off-flavor) is a worldwide problem, affecting both municipal and natural water supplies (Tabachek and Yurkowski 1976; Yurkowski and Tabachek 1980; Yagi et al. 1983). Off-flavor of natural waters is most frequently associated with eutrophic conditions (Persson 1980, 1982; Sivonen 1982; Juttner 1984). Fish can absorb a wide variety of these volatile off-flavor compounds and become unpalatable. In the farm-raised channel catfish (*Ictalurus punctatus*) industry, 50–80% of the fish arriving at the processing plant are affected (S. Marshall, Delta Pride Catfish, Inc., Indianola, MS, pers. comm.). These market-sized fish must be kept at the ponds until the off-flavor subsides; however, this delay has severe economic consequences. The incidence and seasonal severity of off-flavor in culture ponds are influenced by water temperature, fish density, and feeding rates (Brown and Boyd 1982).

Numerous compounds are capable of causing off-flavor in fish (Persson 1984). The most commonly occurring off-flavors in catfish have been described as musty, muddy, or earthy and have been associated with the compounds geosmin and 2-methylisoborneol (MIB) (Lovell 1986; Martin et al. 1987, 1988c). These saturated alcohols are produced by certain species of Cyanobacteria (Izaguirre et al. 1982; Slater and Blok 1983) and actinomycetes (Gerber 1983). They are probably produced by the isoprenoid pathway involved in carotenoid synthesis (Bentley and Meganathan 1981).

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Off-flavor compounds have very low odor thresholds which complicate both their removal from contaminated water and their chemical indentification in water and fish. Recently, a microwave distillation technique was developed to isolate these compounds from fish flesh, enabling more rapid and sensitive analysis than by previous methods (Martin et al. 1987). Using this method, MIB was identified as the common cause of off-flavor in the commercial culture of catfish. The related compounds, 2-methylenebornane and 2-methyl-2-bornene, were also implicated as causes of chronic off-flavor (Martin et al. 1988b). Attempts to purge off-flavor fish of these malodorous compounds have met with limited success.

The disposition of MIB in market-sized channel catfish has not been studied. The present study examines the tissue distribution and clearance of MIB in market-sized channel catfish and the feasibility of depuration for controlling off-flavor caused by MIB.

Materials and Methods

Channel catfish were obtained from local farms where off-flavor was not observed. Fish were individually distributed and acclimated in 90-L aquaria. Water temperature was 25–28°C and pH 8.0–8.2. The fish were fed a commercial diet (32% protein) during acclimation but were not fed during the actual experiment.

2-Methylisoborneol (MIB) was synthesized and purified (99%) according to the method of Snoeyink and Wood (1977). The dehydration compounds of MIB, 2-methylenebornane, and 2-methyl-2-bornene, were synthesized by the procedure of Lapalme et al. (1979).

To determine the tissue distribution and metabolism of MIB, nine catfish (0.4–0.7 kg body weight) were anesthetized in tricaine methanesulfonate (Sigma Chemical Co., St. Louis, MO) solution (0.15 $mg \cdot L^{-1}$), implanted with a urinary catheter (Plakas et al. 1988), and administered MIB intravascularly at the caudal peduncle by syringe. The dosing solution (2 $mg \cdot mL^{-1}$) was prepared in a vehicle of ethanol:Emulphor (polyethoxylated vegetable oil, GAF Corp., New York, NY):saline (1:1:8 by volume). The dosage was 1 $mg \cdot kg^{-1}$ body weight. Urine was collected cumulatively over 2, 6, 12, and 24 h; the volume was recorded, and an aliquot was frozen for subsequent analysis. Three fish were killed at 2, 24, and 96 h and the following tissues and fluids were examined: bile, liver, trunk kidney, muscle, peritoneal fat, and skin (which included subepidermal fat). Blood was drawn from the caudal peduncle using heparinized syringes, and the plasma was separated for analysis. Plasma data were used in determining the sampling intervals for the pharmacokinetic study described below. The entire liver, kidney, and peritoneal fat tissue were weighed for calculation of the percentage recovery of the administered dose in these tissues. Muscle and skin were assumed to comprise 50 and 6% of the total body weight, respectively. All tissues and fluids were stored frozen until analysis.

To determine the pharmacokinetics of MIB in catfish, the dorsal aorta of five fish (0.9–1.0 kg body weight) was catheterized (Kitzman et al. 1988). MIB was administered via the cannula at the same dosage (1 $mg \cdot kg^{-1}$) as in the tissue distribution study. Blood was taken at 0.33, 0.5, 1, 1.5, 2, 4, 8, 12, 18, and 24 h after administration, and the plasma was collected and frozen until analysis. The volume of blood (1 mL) withdrawn at each sampling interval was replaced with an equal volume of heparinized saline.

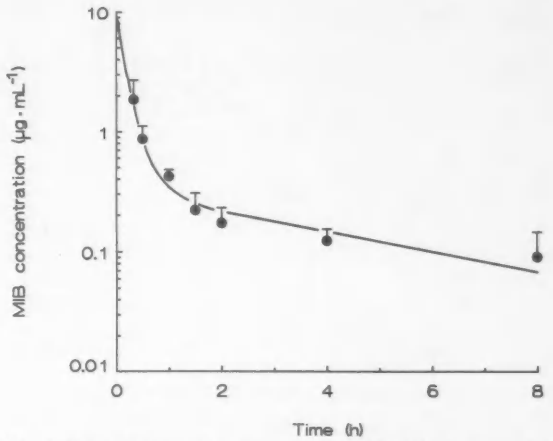

FIG. 1. Plasma concentration (mean ± SD) of MIB after intravascular administration to channel catfish.

TABLE 1. Pharmacokinetic values for 2-methylisoborneol after intravascular administration (1 $mg \cdot kg^{-1}$) in channel catfish.

Parameter[a]	Value
$t_{1/2}$ α (h)	0.14
$t_{1/2}$ β (h)	3.63
V_C ($mL \cdot kg^{-1}$)	118
V_{ss} ($mL \cdot kg^{-1}$)	840
$C1_b$ ($mL \cdot h^{-1 \cdot kg-1}$)	310

[a] $t_{1/2}$ α and $t_{1/2}$ β are the plasma half-lives for the compound in the distribution (α) and elimination (β) phases, respectively; V_C is the apparent volume of distribution of the central comparment; V_{ss} is the steady-state apparent volume of distribution; $C1_b$ is the total body clearance.

MIB was extracted from plasma (0.5 mL) with 0.2 mL of hexane. A 2-μL aliquot of the hexane extract was analyzed for MIB, 2-methylenebornane, and 2-methyl-2-bornene by capillary gas chromatography equipped with flame ionization detector (Martin et al. 1988a). The standard curve was linear in the range 0.25 to 40 $\mu g \cdot mL^{-1}$. Urine was similarly extracted and analyzed. All other tissues were analyzed for MIB and dehydration compounds in duplicate according to the microwave distillation method of Martin et al. (1987, 1988a). The extraction efficiency of MIB from fortified controls was 65 ± 3% for all tissues and body fluids analyzed. The limit of determination in the tissue and fluid specimens were as follows: 0.040 $\mu g \cdot mL^{-1}$ for plasma, urine and bile; 0.005 $\mu g \cdot g^{-1}$ for muscle; and 0.050 $\mu g \cdot g^{-1}$ for peritoneal fat, skin plus subepidermal fat, liver, and kidney. The lower limit of determination for muscle compared with other tissues was related to the larger sample size available. Analysis of tissues from control catfish from the same lot of animals indicated no prior contamination with MIB or dehydration compounds.

Mean plasma concentrations of MIB over time were fitted by using PCNONLIN software (Statistical Consultants, Inc., Lexington, KY) and a two-compartment model. Pharmacokinetic parameters that were not estimated by PCNONLIN were calculated according to the methods of Gibaldi and Perrier (1982).

Results and Discussion

Plasma clearance of MIB from channel catfish was rapid (Fig. 1); MIB was not discernible in the plasma of any fish beyond 12 h after administration. The plasma concentration (C_p) over time (t) was well described by a two-compartment open model in the following equation:

$$C_p = 8.20e^{-5.073t} + 0.309e^{-0.191t}$$

MIB disposition was characterized by short plasma half-lives, very rapid total body clearance (Cl_b) and relatively large volume of distribution at steady-state (V_{ss}) (Table 1). The volume of distribution of the central compartment (V_c) was approximately three-fold greater than the estimated total plasma volume and indicated initial distribution of MIB to tissues outside of the plasma compartment.

MIB was concentrated in the fatty tissues (i.e. skin which included subepidermal fat and peritoneal fat) at levels considerably higher than those in the other tissues (Table 2). Muscle and liver had the lowest concentrations of MIB. The concentration of MIB was highest at 2 h in all tissues except peritoneal fat (maximum values at 24 h). MIB was not detected (below 0.050 $\mu g \cdot g^{-1}$) in the liver of any fish after 2 h, except a high level (0.240 $\mu g \cdot g^{-1}$) occurred in one fish at 96 h. At 2 h following administration, the concentration in the muscle (0.107 $\mu g \cdot g^{-1}$) was slightly less than that of the plasma (0.173 $\mu g \cdot g^{-1}$). The muscle concentrations declined by 64% from 2 to 24 h and 34% from 24 to 96 h.

MIB levels were particularly variable in the fatty tissues; however, this may be partially attributable to differences in relative fat content between fish. For example, the amount of peritoneal fat ranged from 1.2 to 3.2% of total body weight. Muscle concentrations of MIB were less variable between fish.

The skin and muscle contained the highest percentages of the administered dose (Table 2). MIB was not found in the bile. Urinary excretion of MIB was also minor, accounting for less than 6% of the administered dose over 24 h (data not shown). The percentage of the administered dose found in all compartments analyzed was less than 20% at 2 h. Dose recovery and pharmacokinetic data suggest elimination via the gills or rapid biotransformation of MIB.

The dehydration compounds, 2-methylenebornane and 2-methyl-2-bornene, were not found in any tissue or fluid analyzed. Concentrations of 2-methylenebornane and 2-methyl-2-bornene in catfish from off-flavor commercial ponds have exceeded 1 $mg \cdot kg^{-1}$ (Martin et al. 1988b). The absence of these dehydration compounds in the present study suggests that they are not products of metabolism of MIB by catfish.

The concentration of MIB in the edible flesh at 96 h greatly exceeded the threshold odor concentration (0.07–0.55 $\mu g \cdot kg^{-1}$) estimated by Persson (1980). The elimination of MIB from the edible flesh of market-sized catfish appeared slower compared with the rate in fingerlings reported previously (Martin et al. 1988a). Under commercial aquaculture conditions, the accumulation of the dehydration compounds, 2-methylenebornane and 2-methyl-2-bornene, would further complicate elimination of off-flavor because these compounds are more persistent in the edible flesh (Martin et al. 1988b). Alternatives to depuration (e.g. water treatment) may provide more practical solutions to this problem.

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TABLE 2. Tissue concentration and dose recovery (in parentheses) of MIB after intravascular administration at 1 $mg \cdot kg^{-1}$ to channel catfish. Concentration and recovery data are expressed as mean ± SD for three fish per time interval ($\mu g \cdot g^{-1}$ and percent of administered dose, respectively.

Time after dosing (h)	Tissue				
	Skin	Peritoneal fat	Trunk kidney	Liver	Muscle
2	1.470 ± 0.530 (8.8)	0.293 ± 0.250 (0.6)	0.296 ± 0.091 (0.2)	0.095 ± 0.039 (0.1)	0.107 ± 0.034 (5.3)
24	0.413 ± 0.032 (2.5)	0.825 ± 0.501 (1.5)	0.106 ± 0.014 (0.1)	nd[a]	0.038 ± 0.021 (1.9)
96	0.092 ± 0.034 (0.6)	0.211 ± 0.101 (0.4)	nd	m[b]	0.025 ± 0.018 (1.2)

[a]nd, below limit of determination.

[b]Mean value was not calculated because only one of three fish had measurable levels (see Results and Discussion).

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Conversion and Partitioning of Radio-Labelled Mercury Chloride in Aquatic Model Systems

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Regnell, O. 1990. Conversion and partitioning of radio-labelled mercury chloride in aquatic model systems. Can. J. Fish. Aquat. Sci. 47: 548–553.

Conversion and partitioning of radio-labelled inorganic mercury ($^{203}HgCl_2$) was studied in freshwater model systems composed of sediment and water, or water alone, incubated for up to 10 d. The mercury fractions studied were total ^{203}Hg and methyl ^{203}Hg in water and sediment, respectively, and volatilized ^{203}Hg in the gas phase. Water samples were filtered to obtain values for dissolved total ^{203}Hg and methyl ^{203}Hg, respectively. Methylated ^{203}Hg was detected in all systems. Most of the methyl-^{203}Hg was bound to the sediments. Net methyl ^{203}Hg production in a system with reduced sediment was an order of magnitude greater than in the other systems. Volatilization of ^{203}Hg was most rapid in the systems without sediment, while no volatilization took place in sterilized systems.

Nous avons étudié la transformation et la différenciation du mercure inorganique radiomarqué ($^{203}HgCl_2$) dans des systèmes dulcicoles modèles composés de sédiment et d'eau, ou d'eau seulement, avec incubation pouvant aller jusqu'à 10 d. Les fractions étudiées étaient constituées par le ^{203}Hg total et le méthyl-^{203}Hg dans l'eau et le sédiment, respectivement, et le ^{203}Hg volatilisé dans la phase gazeuse. Le filtrage des échantillons d'eau a permis de doser le ^{203}Hg total dissous et le méthyl ^{203}Hg dissous. Le méthyl-^{203}Hg a été détecté dans tous les systèmes. La plus grande partie du méthyl-^{203}Hg était liée aux sédiments. La production nette de méthyl-^{203}Hg dans un système avec sédiment réduit était supérieure d'un ordre de grandeur à celle des autres systèmes. La volatilisation de ^{203}Hg était la plus rapide dans les systèmes sans sédiment, tandis qu'aucune volatilisation ne se produisait dans les systèmes stérilisés.

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Elevated concentrations of mercury in freshwater fish is still a problem in many countries (MacCrimmon et al. 1983; Björklund et al. 1984; Parks et al. 1986; Jackson 1988). Even fish from pristine lakes, with low content of mercury in water and sediment, often contain remarkably high levels of mercury (MacCrimmon et al. 1983). The reverse situation, with heavy mercury contamination and extremely low mercury concentration in fish, is reported for some Swedish lakes receiving mine drainage (Lindeström and Grahn 1982). It is therefore reasonable to believe that the speciation of mercury is crucial for mercury uptake in fish. Analyses of mercury in freshwater fish show, with few exceptions, that essentially all is methyl mercury (Westöö 1972). Methyl mercury, normally constituting less than 1% of the total mercury pool in a lake (Jernelöv et al. 1975), has a remarkable potential for bioaccumulation (Carty and Malone 1979; Boudou and Ribeyre 1985).

Microorganisms methylate inorganic mercury (Jensen and Jernelöv 1969). It is also established that microorganisms reduce Hg^{2+} to Hg^0 and demethylate methylmercury to Hg^0 and CH_4 (methane). These reductions of Hg^{2+} are detoxification mechanisms, but even methylation has been shown to render some protection from Hg^{2+} (Landner 1971; Billen et al. 1974; Schottel et al. 1974; Foster and Ginnity 1985).

The objectives of this study were to construct aquatic model systems suitable for simulating partitioning and speciation of mercury entering a lake and to demonstrate the influence of some environmental variables.

Materials and Methods

Sampling

Undisturbed sediment cores and overlying water (Fig. 1) were taken in July 1987 at a depth of 5 m in Lake Emmahult, a small (20 ha) oligotrophic forest lake, situated in southern Sweden. The lake is not polluted apart from atmospheric deposition. Predatory fish (pike and perch) from the lake show elevated levels of mercury (> 0.5 ppm) (Ohlin 1982). At the sampling depth, water temperature was 16.6°C, oxygen level near saturation (87%), pH 6.4, alkalinity 0.132 meq·L^{-1}, conductivity 11 mS·m^{-1}. The organic content of the sediment was 32% (ignition loss) on a dry weight basis. The sediment cores were transported to the laboratory within 8 h from the time of sampling and incubated at the in situ temperature.

Model Systems

The experiment was performed in the same cylinders that were used for sampling (no transfer of sample), thereby keeping the sediment layers intact. The cylinders, made of acrylic plastic, height = 350 mm, inside diameter = 44 mm, were sealed with butyl rubber stoppers at the bottom and silicone rubber

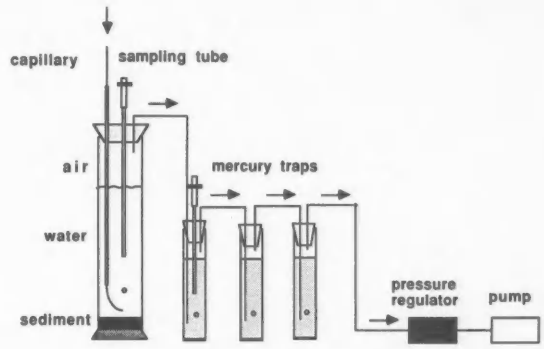

FIG. 1. Model system used in this study.

stoppers at the upper end (Fig. 1). One system was autoclaved and contained in a glass cylinder with silicone rubber stoppers at both ends as these materials were resistant to autoclaving. Incubation temperature was 16 ± 0.5°C and the cylinders were shielded from direct daylight.

The water phases were gently aerated (one bubble every third second). The systems were operated under reduced pressure, so that no leakage of gaseous mercury occurred. The outflowing air passed through three mercury traps containing 0.1 M $K_2Cr_2O_7$ in 2M HNO_3 (Fig. 1).

Six systems contained undisturbed lake sediment (2 cm) with overlying water. Two of these were exposed to higher levels of mercury than the others. Five systems contained only water, and one of these was autoclaved. To keep the autoclaved system sterile, the inflowing air was passed through an 0.2-μm filter (Gelman Sciences).

On day one (one day after sampling), half of the nonsterile systems were ammended with 50 mg·L^{-1} of sterilized tryptic soy broth (TSB) to stimulate microbial activity.

On day three, radiolabelled $HgCl_2$ (6.71 μCi ^{203}Hg/μg Hg) in 0.2 M NaCl was injected into the water (Table 1). At the time of injection, aeration was stopped temporarily, allowing the mercury to spread evenly in the water column, and then resumed.

Measurements

One day after the TSB addition, free oxygen and bacterial activity were measured. The bacterial activity was estimated by measuring ^{14}C-labelled glucose incorporation into bacteria (Tranvik and Höfle 1987). Four samples (10 mL) were taken from each system. One of the samples was used as blank and sterilized with formalin. The samples were incubated with 750 Bq ^{14}C-glucose (90 μg glucose·L^{-1}) in the dark for 2 h. The incubation was ended by formalin addition and the samples were filtered through 0.2-μm cellulose nitrate filters. The filters were washed with distilled water and dissolved in a scintillation cocktail (Packard). ^{14}C-disintegrations were measured with a Beckman 5801 liquid scintillation counter.

During the incubation with ^{203}Hg, water and trap solutions were sampled daily and analyzed with a gamma spectrophotometer (CompuGamma). Disintegrations were recorded in the energy interval over the ^{203}Hg photo peak. Counting efficiency for the sample geometry chosen was 28% based on comparison with LCS which had a counting efficiency of 100% for unquenched samples. Background counts were ≤20 cpm. All count were corrected for radioactive decay.

At the end of the incubation (day 9), concentrations of total ^{203}Hg and methyl-^{203}Hg were determined in the water, porewater (supernatant of sediment centrifuged at 2500 G), and in the sediment. Dissolved forms of mercury were determined after filtration through 0.2-μm filters. Water samples were taken in duplicate and sediment samples in triplicate. The mercury traps were sampled for volatilized ^{203}Hg.

TABLE 1. Model systems used in this study. Notice that systems 3 and 6 were "high level mercury" systems. TSB = tryptic soy broth added at 50 mg/L water. Numbers in parentheses are standard deviations (n = 3). * = see Materials and Methods.

No.	System Category	Hg added (ng/L)	^{203}Hg added (μCi/L)	Bacterial activity* (cpm/10 mL)
1	Sediment/water	992	6.79	290 (40)
2	Sediment/water	810	5.45	170 (7)
3	Sediment/water	49342	71.0	not measured
4	Sediment/water/TSB	400	2.68	8400 (300)
5	Sediment/water/TSB	1024	6.87	7200 (600)
6	Sediment/water/TSB	32895	47.4	not measured
7	Water	942	6.32	300 (50)
8	Water	974	6.53	780 (60)
9	Water/TSB	871	5.84	9800 (900)
10	Water/TSB	934	6.26	5000 (300)
11	Water/audoclaved	1195	8.02	not measured

Methyl-^{203}Hg was extracted from water and sediment by the methods of Furutani and Rudd (1980) and Jacobs and Keeney (1974), respectively. However, the clean up procedure which is imperative prior to GC analysis was found to be unnecessary. To confirm that the radioactivity represented methyl-^{203}Hg, subsamples of the extraction solvent were applied on thin layer plates (silica gel 60 F_{254}, Merck) together with nonlabelled methyl mercury bromide standard. The plates were eluted with either hexane-acetone 3:2 or chloroform-methanol 9:1. R_F-values for methyl mercury bromide were 0.5 and 0.7, respectively. Methyl mercury spots were made visible (bright yellow) by spraying with 0.05% dithizone in chloroform. The spots were removed and ^{203}Hg-disintegrations were measured. To check that isotopic exchange did not occur at the application point nonlabelled methyl mercury bromide standard was applied next to the radioactive sample on one plate.

Results

Bacterial Activity

The TSB additions increased bacterial incorporation of ^{14}C-glucose. One day after the addition, incorporation of glucose increased by one order of magnitude (Table 1), while free oxygen in the water columns had decreased from 80–90% saturation to below 15%. However, at the end of incubation, free oxygen was again at 80–90% saturation perhaps due to algal growth or declining heterotrophic activity. Cylinder leakage can be excluded as the bubbling rate kept constant. The sediment of one of the TSB ammended systems (No. 4) became reduced (black) during the incubation, probably due to higher heterotrophic activity than in the other systems as indicated in Table 1. Why this system behaved differently with respect to heterotrophic activity is unclear.

Recovery of Added Mercury

The average recovery of added mercury from the sediment–water systems was 72% (Table 2). For the systems without sed-

TABLE 2. Partitioning and recovery of total ^{203}Hg in the model systems 1 wk after addition of Hg. S = sediment, W = water, TSB = tryptic soy broth added (50 mg/L), H = "high level Hg," A = autoclaved, n.a. = not analysed.

System Category No.	Percent of total counts				
	Sediment	Unfiltered Water	Pore Water	Air	Recovery
1 S/W	40.6	59.1	0.3	0.0	79
2 S/W	55.3	44.4	0.3	0.0	69
3 S/W/H	34.6	60.6	n.a.	4.8	76
4 S/W/TSB	62.1	36.3	0.1	1.5	83
5 S/W/TSB	67.4	32.0	0.2	0.3	58
6 S/W/TSB/H	40.0	39.3	n.a.	20.7	70
7 W	—	82.6	—	17.4	36
8 W	—	63.4	—	36.6	29
9 W/TSB	—	74.4	—	25.6	23
10 W/TSB	—	86.3	—	13.7	45
11 W/A	—	100.0	—	0.0	74

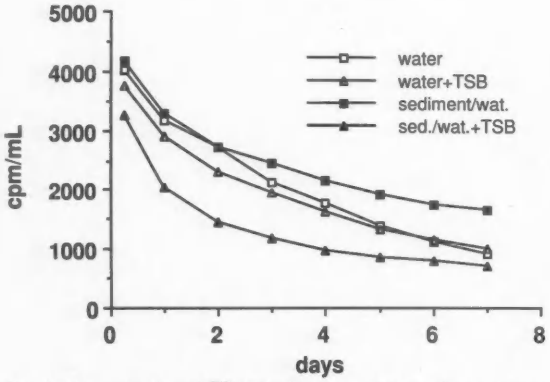

FIG. 2. Concentration of ^{203}Hg in the water of the various systems. The plotted values are averages of measurements in two systems of the same category after mercury addition.

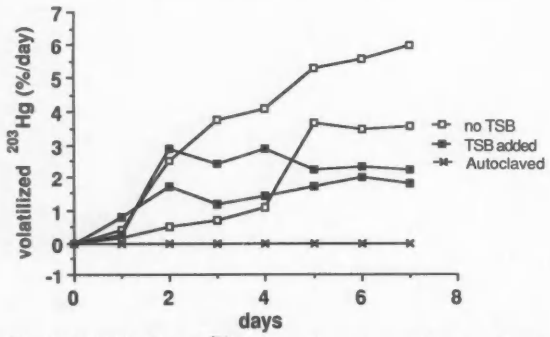

FIG. 3. Volatilization of ^{203}Hg from the systems without sediment. ^{203}Hg volatilized each 24-h period are expressed as percentages of the total ^{203}Hg concentration present in the water at the end of the period after mercury addition.

iment the average recovery was 33%. From the autoclaved system 74% of the mercury was recovered.

Concentrations of total ^{203}Hg in the water decreased exponentially with time (Fig. 2). At the end of incubation, 35–70%

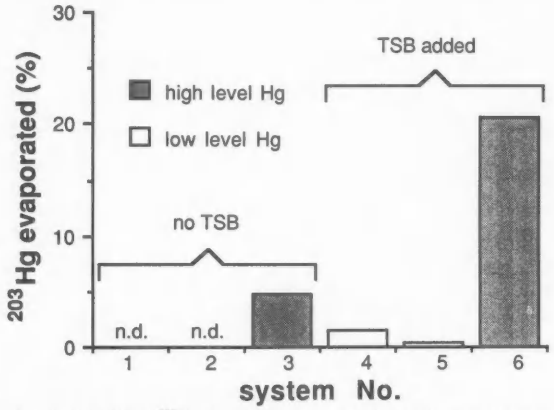

FIG. 4. Volatilized ^{203}Hg found in the traps in the systems containing sediment expressed as percentages of the total ^{203}Hg recovered from the systems. n.d. = not detected.

of the recovered mercury was in the sediment (Table 2). The dissolved fraction of total ^{203}Hg was higher in the oxidized sediment–water systems than in the systems without sediment, with the exception of the autoclaved system, indicating higher adsorption of dissolved mercury to the butyl rubber stoppers than to the oxidized sediment (Table 4).

Volatilization of Mercury

Volatilized ^{203}Hg was found exclusively in the traps positioned first in line, indicating that none of the Hg escaped the sequence of traps. Volatilization was highest in the systems without sediment (Table 2). In the autoclaved system no volatile mercury was detected (Fig. 3). In the sediment–water systems, only small amounts of the added mercury were volatilized except in the "high level" mercury systems (Table 2, Fig. 4). The addition of TSB increased volatilization in the sediment–water systems (Fig. 4).

Methylation of Mercury

Results from the thin layer chromatography confirmed the identity of the methyl mercury. More than 80% of the radioactivity was found in the same spot as the nonlabelled methyl mercury bromide standard. Similar results were obtained regardless of whether hexane-acetone 3:2 or chloroform-methanol 9:1 was used as the eluent. When the radioactive samples were applied next to the nonlabelled standard, 80% of the radioactivity travelled the same distance as the nonlabelled standard.

In the sediment–water systems, most of the methyl-^{203}Hg was found in the sediment, suggesting that the methylation rate was higher in the sediment than in the water (Table 3). TSB addition stimulated methyl mercury production in the sediment–water systems (Table 3, Fig. 5). Methyl mercury production in the system with reduced sediment was much higher than in the other systems (Table 3, Fig. 5).

Mercury in Pore Water

Total ^{203}Hg was lower in the pore water than in the overlying water which suggests that the added Hg had not penetrated the sediment. In the systems with oxidized sediment total ^{203}Hg concentration in the pore water was 18–21% of the concentra-

TABLE 3. Amount of methyl mercury, produced from the added $HgCl_2$, found in different compartments of the system. Values are expressed as the proportion of methyl ^{203}Hg to total ^{203}Hg in the compartment and as absolute amounts in nannograms of Hg. Numbers in parentheses are standard deviations in percent of average value. S = sediment, W = water, TSB = tryptic soy broth added (50 mg/L), H = "high level mercury," A = autoclaved, s.l. = sample lost, n.a. = not analysed. * = one sample. ** = mercury absorbed to the cylinder walls or rubber stoppers is not considered. Further, it is assumed that the volatilized mercury did not contain methyl mercury.

System Category No.	Unfiltered water (%)	Unfiltered water (n g)	filtered water (%)	filtered water (n g)	sediment (%)	sediment (n g)	Total** (%)	Total** (n g)
1 S/W	0.04	0.02 (*)	0.06	0.01 (10)	0.09	0.03	0.06	0.05
2 S/W	s.l.		0.06	0.01 (*)	0.12	0.04 (4)	—	—
3 S/W/H	s.l.		n.a.		0.10	5.3 (1)	—	—
4 S/W/TSB	0.65	0.08 (6)	1.02	0.03 (12)	1.59	0.36 (11)	1.22	0.44
5 S/W/TSB	0.08	0.02 (4)	0.10	0.01 (14)	0.29	0.12 (1)	0.22	0.14
6 S/W/TSB/H	0.14	5.0 (5)	n.a.		0.40	31.0 (2)	0.21	36.0
7 W	0.19	0.05 (21)	0.17	0.01 (6)	—	—	0.16	0.05
8 W	0.11	0.02 (14)	0.14	0.01 (50)	—	—	0.07	0.02
9 W/TSB	0.15	0.02 (0)	0.21	0.01 (40)	—	—	0.11	0.02
10 W/TSB	0.10	0.04 (15)	0.10	0.01 (50)	—	—	0.09	0.04
11 W/A	0.04	0.03 (8)	0.06	0.03 (3)	—	—	0.04	0.03

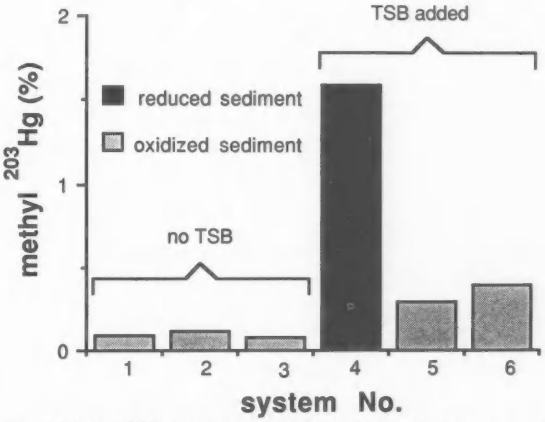

FIG. 5. Methyl-^{203}Hg in the sediment at the end of incubation expressed as a percentage of the total ^{203}Hg in the sediment.

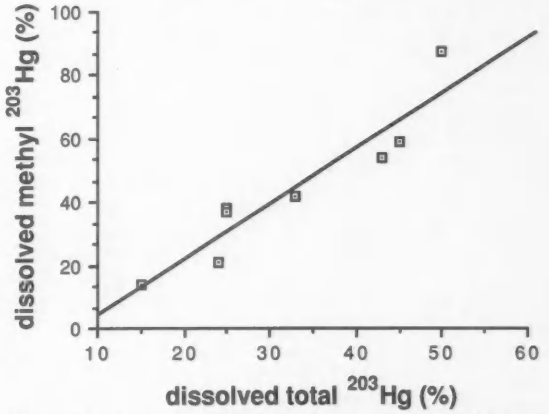

FIG. 6. Dissolved methyl-^{203}Hg (Y) and dissolved total ^{203}Hg (X) expressed as percentages of the concentration of methyl-^{203}Hg and total ^{203}Hg in unfiltered water, respectively. The linear relationship between these variables is given by: $Y = -13.3 + 1.8X$, $r = 0.94$ ($p < 0.001$). The slope (1.8) of the line is >1 ($p < 0.05$).

TABLE 4. Concentrations of methyl $-^{203}$Hg and total ^{203}Hg in filtered water expressed as percentages of the concentration of methyl-^{203}Hg and total ^{203}Hg, respectively, in unfiltered water. S = sediment, W = water, TSB = tryptic soy broth added, s.l. = sample lost.

System Category No.	Percent dissolved: Methyl $-^{203}$ Hg	Percent dissolved: Total ^{203} Hg
1 S/W	59	45
2 S/W	s.l.	60
4 S/W/TSB	38	25
5 S/W/TSB	54	43
7 W	21	24
8 W	42	33
9 W/TSB	37	25
10 W/TSB	14	15
11 W/A	88	50

tion in the overlying water, in the system with reduced sediment only 9%, probably owing to immobilization by sulphide.

No methyl-^{203}Hg was detected in the pore water of the oxidized sediments. In the system with reduced sediment methyl-^{203}Hg concentrations were slightly higher in the pore water (24 000 dpm·L^{-1}) than in the water column (22 000 dpm·L^{-1}).

Dissolved Mercury

In 75% of the systems a greater fraction of methyl-^{203}Hg than of total ^{203}Hg was in solution (Table 4). There was a significant positive correlation between the dissolved fractions of total ^{203}Hg and methyl-^{203}Hg (expressed as percentages of dissolved + particulate total ^{203}Hg and dissolved + particulate methyl-^{203}Hg, respectively). These mercury fractions were significantly correlated ($p < 0.001$) and linear regression resulted in a slope >1 ($p < 0.05$) showing a tendency of higher solubility of methyl mercury compared with total mercury (essentially inorganic mercury) (Fig. 6).

Discussion

The model system described here allows studies of chemical speciation and distribution of mercury in freshwater environments under realistic conditions. By changing physical, chemical, and biological parameters in the systems it is possible to study how different conditions influence the fate of mercury.

An important feature of the model systems is that methylation and volatilization of mercury can be studied simultaneously.

Volatilized mercury is continuously driven off and determined in the traps while methyl mercury in the water column can be determined at regular intervals. Unfortunately, all volatilized mercury collected in the traps are converted to inorganic Hg^{2+}. There are two known forms of volatile mercury in natural waters, elemental mercury and dimethyl mercury. However, according to several studies production of dimethyl mercury can be ignored compared with the production of methyl mercury and the reduction of methyl mercury and inorganic Hg^{2+} into volatile Hg^0 (Spangler et al. 1973; Bisogni and Lawrence 1975; Compeau and Bartha 1984; Kim and Fitzgerald 1986; Baldi et al. 1987). Craig and Moreton (1985) studied the conversion of methyl mercury into dimethyl mercury in sediment ammended with sulphide at 4 $mg \cdot g^{-1}$ (dry wt), as high level of sulphide is known to promote the conversion of methyl mercury to dimethyl mercury. They found that in 13 d only 3% of the methyl mercury was converted into dimethyl mercury.

I find it reasonable to assume that mercury volatilized from freshwater and freshwater sediment is elemental mercury. If there is doubt concerning this assumption it is possible to trap volatile mercury in a solution of Hg^{2+} and Br^- which converts Hg^0 into $HgBr_4^{2-}$ and dimethyl mercury into CH_3HgBr (Spangler et al. 1973).

For some bacteria at least, the enzyme responsible for the reduction of inorganic Hg^{2+} is the same as the enzyme which reduces organomercury compounds subsequent to the splitting off of the organic moiety carried out by another enzyme (Schottel et al. 1974; Foster and Ginnity 1985). Although the relative abundance of bacteria which are capable of demethylation compared with those which only reduces inorganic Hg^{2+} is not known and probably vary as a result of different exposures, elemental mercury evolution may be closely correlated to demethylation. For instance, the absence of elemental mercury evolution, being the case for some of the model systems in this study, indicates that no demethylation has taken place.

It is probably important to expose the model systems to as low levels of mercury as is analytically possible if the objective is to study the speciation of mercury in relatively unpolluted waters. An addition of mercury which increases the original mercury concentration several orders of magnitude could favor mercury resistant microorganisms and/or induce enzyme systems involved in the detoxification mercury (Barkay and Pritchard 1988). Hence, excessive mercury additions to the model systems could give misleading information about the mercury speciation in situ. The present study indicated that "high level mercury" systems behaved quite differently from "low level mercury systems" with respect to mercury volatilization.

The reason for the high rate of volatilization of ^{203}Hg in the systems without sediment is unclear. It is possible that the microbial composition in these systems was different from the microbial composition in the sediment–water systems. The absence of sediment may have affected the exposure situation, favoring mercury resistant bacteria and/or the induction of enzymes capable of converting Hg^{2+} to elemental mercury.

In this study more methyl mercury was produced in reduced sediment than in oxidized sediment which is in accordance with several other studies (Olson and Cooper 1976; Compeau and Bartha 1984; Rudd et al. 1983; Craig and Moreton 1986; Jackson 1988). As the system with reduced sediment volatilized more mercury than the other "low level mercury" systems containing sediment, lower demethylation rate does not seem to have caused the higher production of methyl mercury in the reduced sediment.

Volatilization was totally suppressed in the autoclaved system while all the other systems without sediment volatilized 17–36% of the recovered mercury, indicating microorganisms to play an important role in the emission of mercury from sediment and water to the atmosphere.

Some methyl mercury was found in the autoclaved system. Bartlett et al. (1977) who observed methylation in autoclaved sediment argued that methylating agents, methyl corrinoids which are produced by bacteria, could methylate mercury in a purely chemical reaction. It has been shown in a number of studies that methyl cobalamin can methylate Hg^{2+} abiotically (Bertilsson and Neujahr 1971; Compeau and Bartha 1983; Craig and Moreton 1985).

The low recovery of mercury from the systems without sediment was probably caused by adsorption of mercury to the butyl rubber stoppers, but unfortunately the radioactivity of the stoppers was not measured. Silicone rubber stoppers should be preferred as they are more chemically inert than butyl rubber stoppers. In the sediment–water systems, on average 30% of the added mercury was not recovered and therefore probably adsorbed to the cylinder walls.

Proper evaluation of the influence of different environmental parameters on chemical speciation and partitioning of mercury requires well defined conditions in the model system. Parameters known to affect mercury speciation should be monitored at least at the start and at the end of incubations. In the present study, important sediment parameters as Eh-potentials, sulphide concentrations, initial mercury concentration, and clay content were not measured (Craig and Moreton 1986; Jackson 1988). Therefore, this study serves mainly to illustrate the potential use of the model systems.

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Metabolic Allometry of Larval and Juvenile Yellow Perch (*Perca flavescens*): In Situ Estimates and Bioenergetic Models

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Post, J. R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and a bioenergetic models. Can. J. Fish. Aquat. Sci. 47: 554–560.

Measurements of in situ food consumption and growth rates of young-of-the-year (YOY) yellow perch, *Perca flavescens*, indicated that extrapolations of the metabolic allometry of adult perch to larval and juvenile perch were inappropriate. YOY active metabolism had the same weight dependent slope as adults but was 4.4 times adult standard respiration. Adult active respiration is typically 1–2 times standard. YOY consumption rates were also higher than predicted from adult allometry. Model simulations demonstrate that consumption and growth dynamics of larval and juvenile fish are more sensitive to variation in temperature and prey availability than are adults.

Des mesures réalisées in situ de la consommation de nourriture et du taux de croissance des jeunes de l'année, chez la perchaude *Perca flavescens*, ont indiqué qu'il était inapproprié d'extrapoler l'allométrie métabolique des perchaudes adultes aux larves et aux juvéniles. Chez les jeunes de l'année, le métabolisme actif présentait la même courbe dépendante du poids que chez les adultes, mais la respiration correspondait à 4,4 fois la respiration standard des adultes. Chez ces derniers, la respiration active correspond généralement à 1–2 fois la respiration standard. Le taux de consommation des jeunes de l'année était aussi plus élevé que ne le laissait prévoir l'allométrie par rapport aux adultes. La modélisation montre que la consommation et la dynamique de croissance sont plus sensibles à la variation de la température et de la disponibilité des proies chez les larves et les juvéniles que chez les adultes.

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Early life production dynamics of fish is highly variable and poorly understood (Sissenwine 1984). Consequently, results from field and laboratory studies with adults have been applied to larvae and juveniles, yet it is unknown what the magnitude of the extrapolation errors may be. It is therefore necessary to improve our understanding of the production dynamics of young fish since they are: (1) the basis for future stocks, (2) the primary prey for adult piscivorous fish and (3) significant consumers of secondary production.

An energy budgeting approach has been useful in quantifying the growth dynamics of adult fish in both the laboratory and field (Solomon and Brafield 1972; Elliott 1976; Staples and Nomura 1976; Mills and Forney 1981; Minton and McLean 1982; Brett 1983). Rice and Cochran (1984) used a computer simulation model, derived from metabolic allometry determined in the laboratory to successfully represent the growth dynamics of a field population of adult largemouth bass. This field test of the energy budgeting approach suggested that the technique adequately quantified the growth and consumption dynamics in a natural aquatic community (Rice and Cochran 1984; Kerr and Dickie 1985).

The goals of this research are to use an energy budgeting approach to understand the growth and consumption dynamics of young-of-the-year (YOY) yellow perch (*Perca flavescens*) and to test if the allometric metabolic functions from an adult yellow perch bioenergetic model (Kitchell et al. 1977) adequately represents the observed YOY dynamics.

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Materials and Methods

In Situ Growth and Consumption Rates

YOY yellow perch were sampled in Lake St. George, Ontario (43°57′N, 70°25′W) during seven 24-h periods, in the spring and summer of 1982. Collections were made at approximately 3-h intervals during each 24-h experiment.

Limnetic larvae were sampled with a Miller sampler (Miller 1961) fished at 0.5 and 1.5-m depths as described in Post and McQueen (1988). For each 3-h interval, five stomachs were examined from fish taken from the zone that contained the largest proportion of the population calculated on a volumetric basis. Juveniles nearshore were collected with a 30-m long 2-m deep fine mesh (1.0 × 0.5 mm) beach seine. During each 3-h interval, two beach seine sites were randomly chosen from the 12 possible sites. Five specimens were randomly chosen from each beach seine site for stomach analysis. If sufficient specimens were not captured at a particular site, additional specimens were collected at additional randomly chosen sites.

Fresh lengths and mass were calculated from measurements of preserved samples. Seasonal growth was determined from a regression of fresh length on Julian date and a fresh length to fresh mass curve.

Feeding periodicity was determined for each of the seven 24-h experiments. Whole intestinal tracts were removed, blotted, and weighed to the nearest 0.1 mg. The relationship between body mass and the weight of an empty intestinal tract (EIW) was determined. The intestinal tract content weight (ICW) was calculated by subtracting the predicted EIW from the observed

gut weight. Feeding periodicity was expressed as the change in the ratio of food weight to body weight throughout each 24-h period. Evacuation rates were calculated from the decline in intestinal tract content weight as a proportion of body mass during nonfeeding periods assuming an exponential evacuation rate. Consumption rates were calculated from the feeding periodicity curves and evacuation rates following the method of Elliot and Persson (1978).

To calculate confidence intervals on the total daily consumption estimates, a mean time-weighted food weight as a proportion of body weight and a pooled standard error were calculated for each 24-h experiment. A proportional error was calculated by dividing the product of the pooled standard error times the *t*-score by the mean time weighted food weight as a proportion of body weight. The upper and lower confidence intervals are the product of the total daily consumption estimate ± the proportional error.

Bioenergetics Model

The yellow perch bioenergetics model used was based on those of Kitchell et al. (1977) and Hewett and Johnson (1987). The model assumed that the sole source of energy was food consumption and that all energy consumed is metabolized through respiration, lost through waste production, or accumulated as growth. The units modelled are energy on a weight specific basis ($cal \cdot g^{-1}$ wet mass). The caloric densities of the larval and juvenile yellow perch and their invertebrate prey are approximately 600 $cal \cdot g^{-1}$ wet mass (Post 1988; Treasurer 1989).

Consumption rate is modelled as a function of body mass, temperature, and prey availability. Respiration rate is modelled as a function of body mass, activity, temperature, and specific dynamic action. Waste losses are modelled as a constant proportion of consumption. This differs from Kitchell et al. (1977) but follows the form of Rice et al. (1983), as was suggested by the sensitivity analysis conducted on the original model by Bartell et al. (1986). The sum of energy losses to egestion, F, and excretion, U, are temperature independent (Kitchell et al. 1977).

The coefficients used in the model were derived from a variety of sources (see Kitchell et al. 1987; Hewett and Johnson 1987) but in all cases were from studies of adult fish. The model based on these coefficients will be referred to subsequently as the adult perch model (Table 1). Modifications made to this table of coefficients for application to YOY perch will be referred to as the YOY perch model.

Maximum Growth and Consumption Rates

Growth experiments were conducted in enclosures that were 8 m diameter and 15 m deep. Two enclosures were used in 1982 and four in 1985 in Lake St. George. For a detailed description of the enclosures and their limnological characteristics see Post (1984) and Post and McQueen (1987). YOY yellow perch were stocked into the fish-free enclosures in spring of each year at densities ranging from 6000–36 000 $fish \cdot ha^{-1}$. A subsample of the perch in each enclosure were measured and weighed 3–5 times throughout the experiment. Daily growth rates on a wet weight basis were calculated from von Bertalanffy growth in length curves and length–weight regressions for each enclosure.

Zooplankton abundance in the enclosures was controlled by the density and biomass of yellow perch stocked (Post and McQueen 1987). Zooplankton were sampled weekly and biomass estimated using methods presented in Post and McQueen (1987).

Daily consumption rates for the yellow perch in the enclosures were determined using the YOY perch bioenergetics model with daily growth and mean epilimnetic temperature as inputs.

Results

In Situ Growth and Consumption Rates

Daily growth rates were derived from growth in length and length–weight relationships (Fig. 1). Daily consumption rates were calculated from feeding periodicity curves (Fig. 2). ICW, although variable, was equally high from dawn to dusk, suggesting that the larval and juvenile yellow perch fed throughout daylight hours. The periodicity curve for May 27 differs in that it shows limited variation between individuals during the nine sampling periods and little variation between sampling times. May 27 and early May 28 were overcast with constant rainfall. Daytime light levels were substantially lower than on other sampling days and may have caused a reduction in feeding activity during the day.

Evacuation rates were calculated directly from the feeding periodicity curves assuming that there was a period of nonfeeding. This criterion appears to be met for the June 3 to

TABLE 1. Parameter values for the adult and young-of-the-year perch bioenergetics model (Kitchell et al. 1977; Hewett and Johnson 1987; this study).

Symbol	Parameter description	Adult	YOY
	Consumption function		
CA	Intercept for maximum consumption	0.25	0.51
CB	Slope for maximum consumption	−0.27	−0.42
CTO	Optimum temperature for consumption	23	29
CTM	Maximum temperature for consumption	28	32
CQ	Slope for temperature dependence of consumption	2.3	2.3
	Respiration function		
RA	Intercept for maximum standard respiration	0.035	0.035
RB	Slope for maximum standard respiration	−0.20	−0.20
RTO	Optimum temperature for standard respiration	28	32
RTM	Maximum temperature for standard respiration	33	35
RQ	Slope for temperature dependence of standard respiration	2.1	2.1
ACT	Active respiration multiplier	1.0–2.0	4.4
S	Specific dynamic action coefficient	0.15	0.15

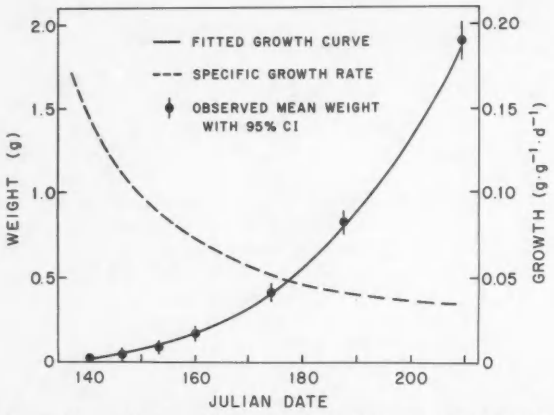

FIG. 1. Observed mean weights, fitted growth curve, and calculated specific growth rate for young-of-the-year yellow perch in Lake St. George.

July 28 period when postdusk feeding is limited. Negative exponential curves were fitted to the maximum rate of decline in ICW at dusk for the June 3 to July 28 experiments (Fig. 2). The relationship between evacuation rates and body mass and temperature for those dates was:

$$R = -3.202 - 0.5093 \text{ Ln } W + 0.1710 \text{ TEMP } (n=5, r^2=0.94)$$

where R is the negative exponential evacuation rate, W is wet mass in grams, and TEMP is mean temperature (°C) in the surface 2 m of Lake St. George. Consumption rates were calculated using predicted evacuation rates for May 20 and May 27 and fitted rates for the other five dates (Table 2).

Daily consumption rates were highest for the smallest larvae and lowest for the largest juveniles, with substantial variation between these extremes (Table 3). Individual estimates were variable, typical of consumption estimates because of variability among individuals. The consumption estimate for May 27 is an outlier, indicating that the low and relatively invariant light levels reduced the feeding intensity and total daily consumption of the yellow perch larvae.

Bioenergetics Model

The relationship between the respiration rates and body mass calculated from the field data was:

$$\text{RESPIRATION}_{20°C} = 0.0962\, W^{-0.216} \ (N=6, r^2=0.71)$$

$$\text{RESPIRATION}_{RTO} = 0.172\, W^{-0.216}$$

where respiration is in grams per gram per day and body mass, W, in grams (Fig. 3). Since the slope does not differ significantly from -0.20 ($t=-0.2180$, $p>0.05$), the general allometric relationship (Kitchell et al. 1977) is applicable to YOY yellow perch over two orders of magnitude in mass.

Active respiration in adult perch is typically 1–2 times the standard respiration (Solomon and Brafield 1972). Active respiration of YOY yellow perch in the field calculated from the Lake St. George growth and consumption data is 4.4 times the standard respiration of adult perch (Table 1, Fig. 3).

A comparison between in situ consumption estimates and model predictions using ACT = 4.4 suggests that the modified

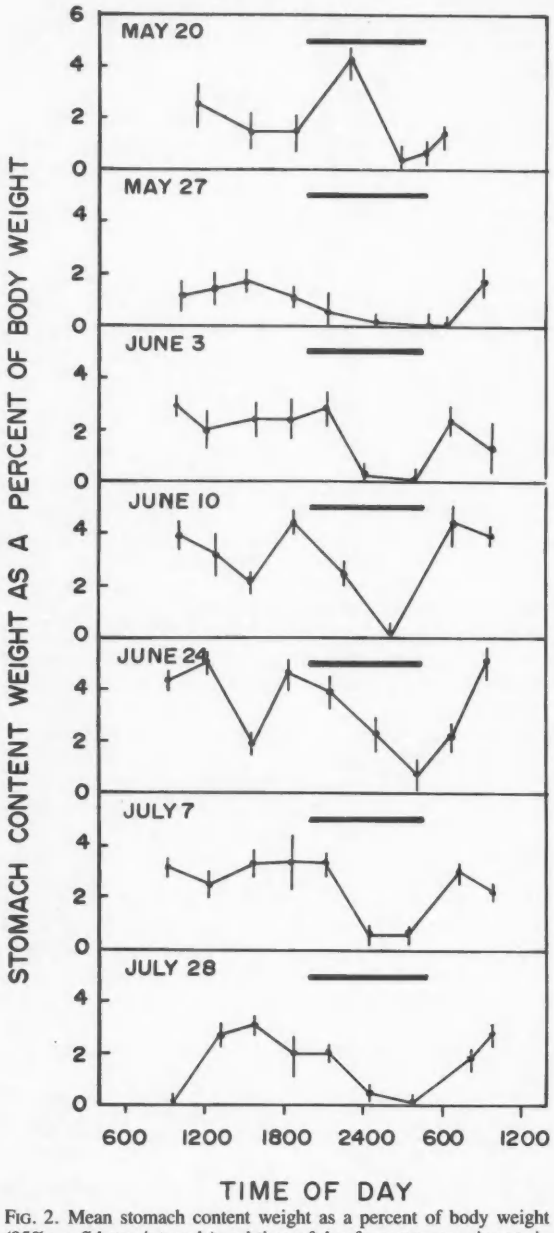

FIG. 2. Mean stomach content weight as a percent of body weight (95% confidence intervals) and time of day for seven experiments in Lake St. George. Hours between sunset and sunrise are indicated by horizontal bars.

model simulates the field measurements (Fig. 4A). This is not a goodness-of-fit test of the model because the observations and predictions are not independent, but the simulation allows several observations. The May 27 "rainy day" in situ estimate is substantially lower than that predicted by the model. The variability about the in situ consumption estimates is much greater than that about the model predictions. The in situ estimates are based on the variation in ICW between few individuals whereas

TABLE 2. Negative exponential evacuation rates (R) calculated from the postdusk decline in intestinal content weight and predicted by the temperature and body mass dependent model. Temperature is the mean temperature of the surface 2 m of Lake St. George.

Date	Mean weight (g)	Temperature (°C)	Evacuation rate (R)	
			Calculated	Predicted
May 20	0.0217	16.6	—	1.59
May 27	0.0480	16.3	—	1.16
June 3	0.0947	16.9	0.93	0.88
June 10	0.170	17.3	0.57	0.65
June 24	0.409	17.9	0.34	0.32
July 7	0.846	21.4	0.57	0.54
July 28	1.95	23.6	0.48	0.50

TABLE 3. Measured in situ daily consumption rates for young-of-the-year yellow perch in Lake St. George. Mean intestinal content weight (ICW) and pooled standard error were used to calculate confidence intervals as described in the text.

Date	N	Mean ICW ($g \cdot g^{-1}$)	Pooled standard error	Consumption Rate (95% C.I.) ($g \cdot g^{-1} \cdot d^{-1}$)	
May 20	35	0.0173	0.00299	0.653	0.424–0.882
May 27	43	0.0084	0.00181	0.228	0.128–0.327
June 3	45	0.0179	0.00259	0.351	0.249–0.453
June 10	37	0.0304	0.00256	0.406	0.336–0.457
June 24	83	0.0335	0.00187	0.271	0.241–0.302
July 7	90	0.0246	0.00201	0.334	0.280–0.389
July 28	85	0.0178	0.00152	0.219	0.164–0.273

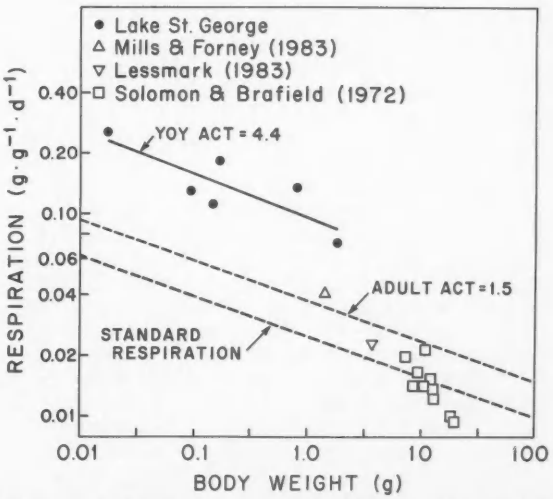

FIG. 3. In situ Lake St. George respiration allometry for young-of-the-year yellow perch calculated from an energy budget. The fitted regression has an intercept 4.4 (ACT) times adult standard respiration. Adult active respiration of 1.5 times standard, experimental data of Solomon and Brafield (1972) and Mills and Forney (1981) and respiration calculated using an energy budget from experimental growth and consumption data from Lessmark (1983) are presented. All data has been scaled to 20°C using the temperature dependence function from Kitchell et al. (1977).

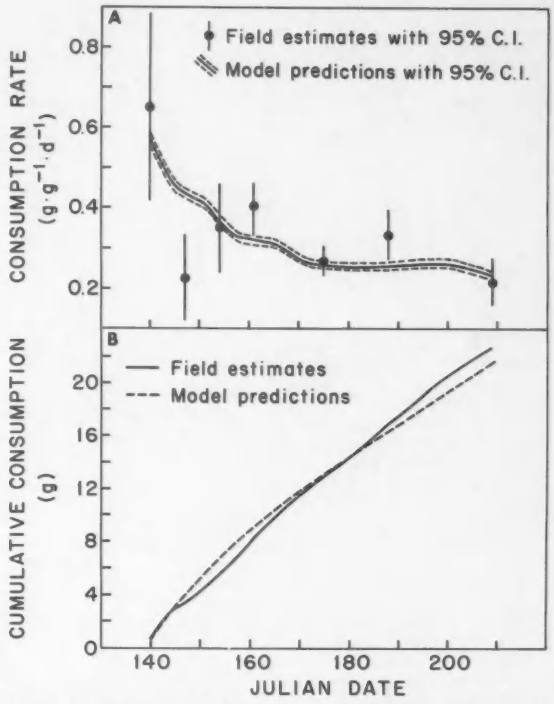

FIG. 4. (A) In situ consumption rates of young-of-the-year yellow perch in Lake St. George and model predictions from in situ measurements of growth and temperature and the YOY respiration model. (B) Cumulative consumption based on the above field estimates and model predictions.

variation in the model predictions are based on the variability in body size of larger numbers of individuals. Since growth is cumulative and the daily growth data used in the model is integrated over time, the model can't predict day to day variability in consumption, but it can accurately predict cumulative consumption (Fig. 4B).

Maximum Growth and Consumption Rates

The model parameter P (observed consumption rate as a proportion of maximum consumption rate (CMAX)) varied from approximately 0.89–1.47 during the simulation presented in Fig. 4. A value greater than 1.00 means that CMAX as specified in the model is too low. In the original model (Kitchell et al. 1977), CMAX was parameterized using data for adult percids (Solomon and Brafield 1972; Kelso 1972; Swenson and Smith 1973). Therefore, extrapolation to larvae and juveniles ranging in weight from 0.02–2.00 g is inaccurate.

Body size of young-of-the-year yellow perch in the six enclosures in the fall ranged from 1–13 g, the largest of which were substantially greater than those reported in the literature (Pycha and Smith 1955; Ney and Smith 1975; Keast 1977; Nielsen 1980) or than observed in five southern Ontario lakes (Post 1987). This indicates that the high prey abundance in enclosures stocked at low fish densities allowed for near maximal growth. Therefore data from the enclosure growth experiments were used to redefine the maximum consumption function. The YOY model was used to calculate daily consumption rates for yellow

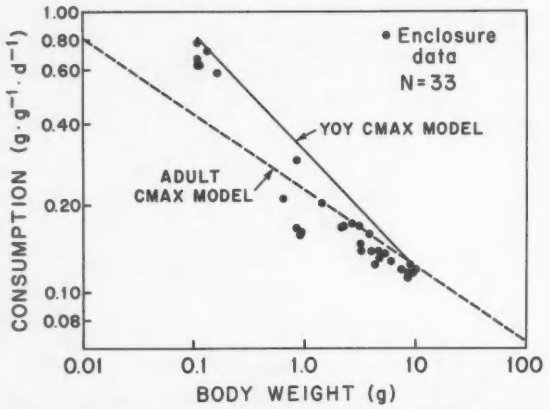

FIG. 5. In situ maximum consumption allometry calculated from an energy budget for young-of-the-year yellow perch growth in Lake St. George enclosures and as modelled in Kitchell et al. (1977) adult model.

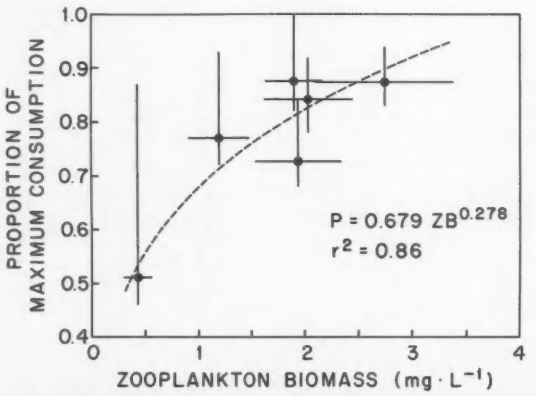

FIG. 6. Relationship between mean zooplankton biomass (*ZB*) and the mean proportion of maximum consumption (*P*) predicted by the YOY model for the six Lake St. George enclosures. Means, ranges, least squares regression, and coefficient of determination are indicated.

perch in each enclosure given observed growth rates and temperature for each date on which mean body size was measured. Each estimate was scaled to 20°C. The line with the lowest intercept value that encompassed all calculated consumption rates was assumed to be the allometric relationship between CMAX and body mass (Fig. 5):

$$\text{CMAX}_{20°C} = 0.32\, W^{-0.42}$$

$$\text{CMAX}_{\text{CTO°C}} = 0.51\, W^{-0.42}$$

where CMAX is in units of grams per gram per day at 20°C or at optimum temperature for consumption (CTO) and W is in grams. This modified CMAX function differs in both slope and intercept from the adult model (Table 1). Reanalysis of the perch growth and temperature data from Lake St. George using the modified CMAX function yielded P values of 0.47–1.00 indicating that the modification successfully incorporated the observed mass versus consumption allometry.

Rice and Cochran (1984) suggested that the bioenergetic parameter P, the proportion of maximum consumption realized, provides a measure of food availability, or the converse, a measure of the degree of food limitation experienced. To test this idea, the mean proportion of maximum consumption for each enclosure was related to the mean zooplankton abundance in that enclosure (Fig. 6). Variation in zooplankton biomass amongst the enclosures explained 84% of the variance in the proportion of maximum consumption attained suggesting that P is a reasonable measure of prey availability as it constrains growth.

Discussion

The allometric functions of respiration and consumption for adult yellow perch are inappropriate for YOY yellow perch. Active respiration for YOY yellow perch in Lake St. George was 4.4 times standard respiration for adult perch and is consistent with the hypothesis that ontogeny of active respiration is a step function, the change occurring after the first year of life. Ware (1975) and Dabrowski et al. (1988) also suggested that active respiration of larval fish at optimal swimming speeds is 3 and 5 times standard respiration. Mills and Forney's (1981) respiration measurements were intermediate between the Lake St. George YOY active respiration estimates and active respiration of adult perch (Fig. 3). The discrepancy may be due to the restriction of normal activity in the respirometer in their experiment. The ontogeny of maximum consumption rates in the enclosure experiments is consistent with the hypothesis of a gradual ontogeny throughout the first growing season (Fig. 5). More data across a wide range of sizes is necessary, but it is clear that respiration and consumption rates of YOY perch are higher than those predicted by extrapolation of adult allometry.

High metabolic rates of young fish accelerate the utilization of body energy stores and therefore reduce time to starvation in situations of inadequate food supply. The larval starvation hypothesis (Lasker 1975) may be the critical mechanism in recruitment success of species with small bodied larvae (Hunter 1981; Miller et al. 1988). Also, the over-wintering young of some temperate freshwater species suffer starvation which may be the critical factor in population viability toward northern limits of the range (Shuter et al. 1980; Post and Evans 1989).

The importance of a consumer in a community is related to the magnitude of energy fluxes. High consumption rates by young fish produce the potential for consumer control of prey populations. There is controversy concerning the potential impact of larval fish on plankton community dynamics. It has been suggested that larval fish are "too dilute" to have significant impacts (Cushing 1983) but even low densities may have significant predatory impacts because of their high consumption rates. For example, at optimal temperature and maximum consumption rates, for equal biomasses of yellow perch larvae (0.01 g) and adults (100 g), the larvae consume approximately 70 times the biomass of prey consumed by the adults (Fig. 7). Another flux that may be important in community dynamics is nutrient recycling which would be approximately proportional to consumption. These direct and indirect effects of fish predation on zooplankton and phytoplankton communities can be substantial (Threlkeld 1987; Mills et al. 1987; Crowder et al. 1988). Also small fish are sensitive to environmental variation and prey dynamics because of the high rate of their metabolic processes. For example, consumption and growth rates of small bodied fish are more sensitive to variation in temperature than are those rates for larger fish (Fig. 7). The sensitivity of growth

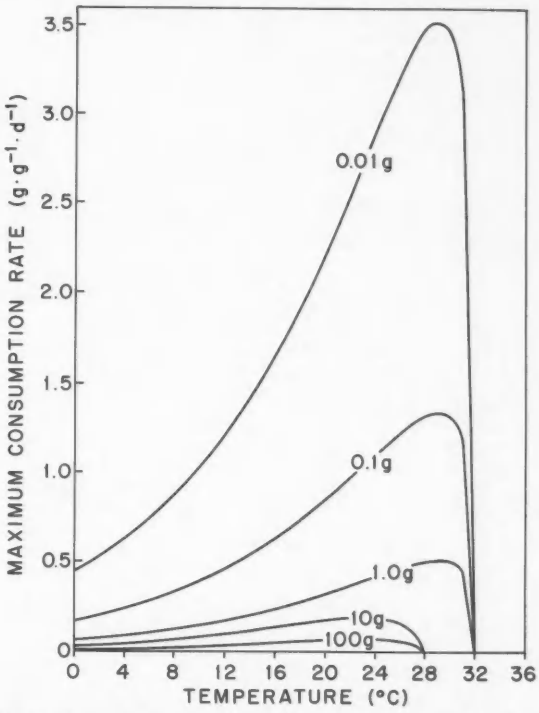

FIG. 7. Temperature dependence of maximum consumption rates ($P = 1$) for young-of-the-year perch (0.01, 0.1, 1 g) and adult perch (10, 100 g) using the parameters in Table 1.

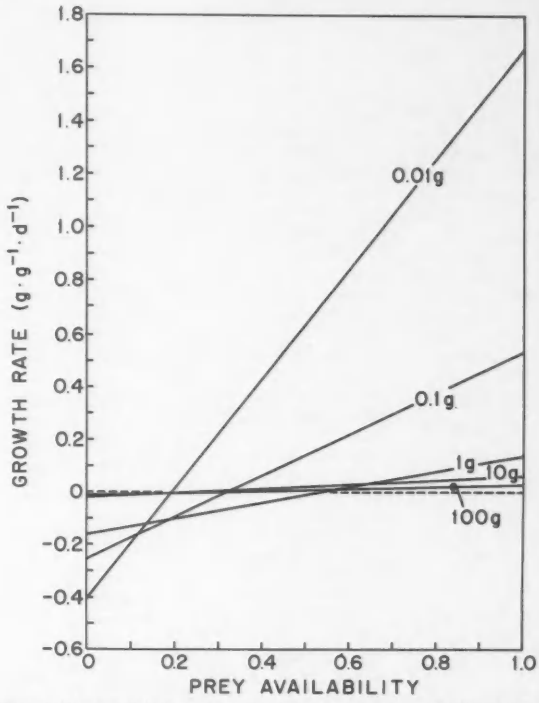

FIG. 8. Relationship between growth rate and prey availability (P) at optimum temperature for consumption for young-of-the-year perch (0.01, 0.1, 1 g) and adult perch (10, 100 g) using the parameters in Table 1.

rate to changes in prey availability is also greater in small than in large fish (Fig. 8). Therefore density dependent competitive interactions are more likely to be observed in younger year classes.

This bioenergetics modelling approach provides a quantitative measure of prey abundance, P, scaled to the energetic demand of the fish (Rice and Cochran 1984). The asymptotic functional response between prey availability and P in the enclosure experiment would not have been discerned if growth rate was the metric since growth rate is also functionally related to temperature and body size. Use of P as the performance metric allows comparisons between situations in which these confounding variables differ.

This study indicates that the metabolic allometry of larval and juvenile fish can not be inferred from adult fish allometry. The accelerated rates of metabolism in young fish magnify their ecological significance in communities as predators, competitors, and recyclers. The bioenergetics modelling approach provides a quantitative tool for examining these processes and integrating them into models of population and community dynamics.

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Age at Sexual Maturity and Pregnancy Rates of Harbour Porpoises *Phocoena phocoena* from the Bay of Fundy

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Age at sexual maturity and pregnancy rate were estimated from a sample of 108 female harbour porpoises *Phocoena phocoena* killed incidentally in a commercial gill net fishery in the Bay of Fundy during July–September, 1985–88. Estimates of sexual maturity ranged from 3.15 to 3.44 yr, depending on the method used; few individuals older than 7 yr of age were present in the sample. The mean age at first pregnancy was 3.76 yr. Pregnancy rate was estimated using two methods: (1) considering the entire sample and using the presence of a corpus luteum as indicative of pregnancy, and (2) by considering the sample collected after implantation and using the presence of a foetus as the criterion of pregnancy. Estimated pregnancy rates using these two methods were 0.86 and 0.74, respectively. Many young females failed to conceive in their first year or two of sexual maturity, but most older females in the sample were pregnant. These high pregnancy rates are indicative of annual reproduction in this population.

L'âge à la maturité sexuelle et le taux de gestation ont été calculés à partir d'un échantillon de 108 femelles de marsouin commun (*Phocoena phocoena*) tuées par accident dans une pêcherie commerciale aux filets maillants de la baie de Fundy, entre juin et septembre, entre 1985 et 1988. Les estimations de l'âge à la maturité sexuelle donnaient une fourchette de 3,15 à 3,44 ans, selon la méthode employée; rares étaient les individus de plus de 7 ans dans l'échantillon. L'âge moyen à la première gestation était de 3,76 ans. Le taux de gestation a été estimé selon deux méthodes : 1) considération de l'ensemble de l'échantillon, la présence d'un corps jaune étant indicatrice de la gestation; 2) considération de l'échantillon après implantation, la présence d'un foetus étant considérée comme critère de gestation. Les taux de gestation estimés selon ces deux méthodes étaient respectivement de 0,86 et 0,74. De nombreuses jeunes femelles n'ont pas conçu pendant leurs deux premières années de maturité sexuelle, mais la plupart des femelles plus âgées étaient gestantes. Ces taux élevés de gestation sont indicatifs de la reproduction annuelle dans cette population.

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Age-specific reproductive rates are essential components of models currently used to describe the dynamics of vertebrate populations (Eberhardt 1985). In marine mammals, age at sexual maturity and pregnancy rate are the reproductive parameters most frequently used to assess changes in the dynamics of exploited populations (Eberhardt and Siniff 1977).

Harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy and Gulf of Maine are captured incidentally in several groundfish gill net fisheries (Read and Gaskin 1988). Although the magnitude of both incidental catches and population size are unknown, the level of mortality is sufficient to warrant concern over the population's status (Read and Gaskin 1988).

Little is known about age-specific reproductive rates in the harbour porpoise. In the Bay of Fundy, age at sexual maturity is believed to occur at age three or four and few individuals live longer than 7 yr (Gaskin et al. 1984). Age-specific pregnancy rates have not been calculated, but the reported proportion of mature females carrying a foetus was only 0.24, surprisingly low for a relatively short-lived mammal with a litter size fixed at one (Gaskin et al. 1984).

The low proportion of pregnant females reported in previous research may be attributable to the effect of reproductive seasonality. In most studies of pregnancy rate, the presence of a foetus is used as the criterion of pregnancy (e.g., Gaskin et al. 1984). If sampling occurs prior to implantation, however, the pregnancy rate will be underestimated because many females will be sampled before the foetus has implanted in the uterus. Recent studies have shown that harbour porpoises in the Bay of Fundy ovulate and conceive in late June, but foetuses are not detectable until early August (Read 1990). The only previous study of harbour porpoise pregnancy rate in the Bay of Fundy included specimens collected from May to September (Gaskin et al. 1984), and thus underestimated the actual pregnancy rate.

In this paper I estimate mean age at sexual maturity and age-specific pregnancy rates for female harbour porpoises in the Bay of Fundy, using samples collected from animals killed incidentally in commercial gill net fisheries. Pregnancy rates are estimated by two methods, both of which account for the effects of reproductive seasonality on the detection of pregnancy.

Methods

The sample consisted of 108 female harbour porpoises captured incidentally in commercial groundfish gill nets in the Bay of Fundy between July and September, 1985–88 (Read and

Gaskin 1988). To account for the seasonality of ovulation and conception (Read 1990), only porpoises captured after 01 July were included in the sample.

Each specimen was examined during a field necropsy in which standard length (American Society of Mammalogists 1961) was measured. Evidence of lactation was obtained by pressing and cutting the mammary glands. The uterus was examined carefully for the presence of a foetus, particularly if a corpus luteum was present on one of the ovaries.

Ovaries were removed and preserved in 10% neutral buffered formalin (NBF). In the laboratory, the ovaries were sliced by hand to obtain sections 1–3 mm thick. The sections were then examined under a dissecting microscope to count corpora albicantia. Corpora atretica were not included in total corpora counts, as they arise from nonovulatory events (Perrin and Donovan 1984). Terminology for ovarian morphology and reproduction follows that described by Perrin and Donovan (1984).

Five teeth were removed from the mid-section of each mandible and preserved in 10% NBF or 70% ethanol. Age estimates were obtained from counts of growth layer groups in thin, longitudinal sections of teeth, prepared by hand-grinding with 320-grit carborundum powder (Gaskin and Blair 1977). The number of growth layer groups in the dentine was counted by examining the sections under transmitted light. Estimated age corresponds to the number of completed growth layer groups (International Whaling Commission 1980). The sections were examined independently by two observers, without access to information on the size or reproductive status of the specimen. If the two age estimates for a specimen differed, the sections were reexamined by both observers. If the second reading did not produce identical estimates, the observers examined the section together and reached consensus on the number of growth layer groups.

The presence of a corpus albicans or corpus luteum was used as the criterion of sexual maturity. Mean age at sexual maturity was estimated from age-specific ovulation rates using the method of DeMaster (1978). Mean age of first-time ovulators was estimated by calculating the mean age of females possessing only a single corpus albicans or corpus luteum. Mean age at first pregnancy was estimated from age-specific pregnancy rates, following DeMaster (1978).

Many females were examined after conception but before implantation had occurred, as evidenced by the presence of a corpus luteum without a foetus visible in the uterus. Therefore, two methods of assessing pregnancy were used: one using the presence of a corpus luteum as the criterion of pregnancy and the second using the presence of a foetus in the uterus. The first method employed the entire sample, but the latter method considered only females collected after most implantation had occurred after 05 August (Read 1990). Pregnancy rate was calculated as the proportion of pregnant females in the sample of mature specimens.

Statistical procedures were performed using SAS/STAT (SAS Institute 1985).

Results

The proportion of mature individuals in each age-class is presented in Table 1. No calves or yearlings showed any evidence of past ovulation, but increasing proportions of the 2, 3, and 4-yr age-classes were mature. All animals aged five and older (n = 24) were both sexually mature and pregnant, based on the presence of a corpus luteum.

TABLE 1. Age-specific reproductive rates in female harbour porpoises from the Bay of Fundy. Column headings refer to sample size for each age-class (N), the number of mature females (M), the number and proportion of pregnant females (P), and the number and proportion of lactating females (L). Proportions were estimated as the fraction of mature females. Pregnancy was assessed by the presence of a corpus luteum.

Age	N	M	P		L	
0	9	0	0	—	0	—
1	19	0	0	—	0	—
2	22	5	1	0.20	0	0.00
3	22	11	8	0.73	3	0.27
4	12	10	10	1.00	5	0.50
5	11	11	11	1.00	9	0.82
6	7	7	7	1.00	5	0.71
7	4	4	4	1.00	4	1.00
8+	2	2	2	1.00	1	0.50
	108	50	43	0.86	27	0.54

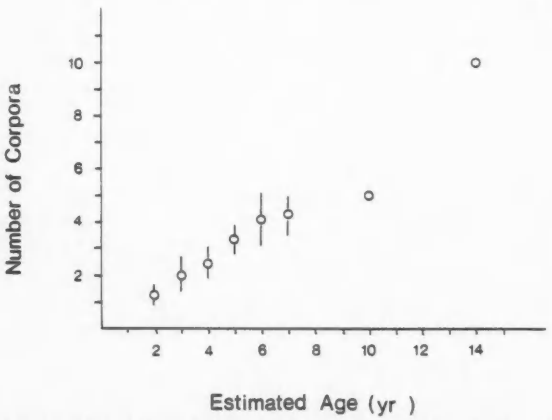

FIG. 1. Age-specific ovulation rate of harbour porpoises in the Bay of Fundy. Data points represent mean number of corpora albicantia and lutea for mature females of each age-class, with accompanying standard error bars. Data points without error bars represent single specimens. The relationship between corpora count and estimated age is significant (R^2 = 0.47, P = 0.0001) and described by: $Y = -0.76 + 0.66(X)$, where X is estimated age in years.

Thirteen females possessed only a single corpus in their ovaries and were assumed to have been sampled in the year in which they first ovulated. The mean age of these animals (estimated mean age of first ovulation) was 3.15 (SD = 1.14). Mean age at sexual maturity, calculated using the method of DeMaster (1978), was 3.44 (SD = 0.182), with a 95% confidence interval of 3.08–3.80.

Several females had ovulated once but were not pregnant at the time of sampling, based on the presence of a corpus luteum (Table 1). These females were younger (X = 2.25, SD = 0.50, n = 4), than those which became pregnant following their first ovulation (X = 3.56, SD = 1.13, n = 9) ($T = -2.17$, P = 0.05). Mean age at first pregnancy, using the method of DeMaster (1978), was 3.76 (SD = 0.160), with 95% confidence limits of 3.46–4.08.

Young females (age-classes 2, 3, and 4) often ovulated more than once each year, sometimes without achieving conception. The mean number of corpora present in ovaries of mature 3-yr-

TABLE 2. Age-specific pregnancy rates of harbour porpoises from the Bay of Fundy, using the presence of a foetus as the criterion of pregnancy. Column headings refer to sample size for each age-class (N), the number of mature females (M), and the number and proportion of pregnant females (P). Proportions were estimated using the sample of mature females. Only porpoises collected after 05 August are included.

Age	N	M	P	
0	8	0	0	—
1	10	0	0	—
2	16	4	0	0.00
3	17	8	5	0.62
4	9	8	7	0.88
5	6	6	6	1.00
6	5	5	5	1.00
7	3	3	2	0.67
8+	1	1	1	1.00
	75	35	26	0.74

old females was 2.0 (SD = 1.33, $n = 10$)), with some individuals possessing as many as five. The number of corpora present in each sexually mature individual was significantly ($F = 42.3$, $P = 0.0001$, $R^2 = 0.47$) correlated with age:

$$(1)\ Y = -0.76 + 0.66(X)$$

where X is estimated age in years (Fig. 1). The slope of this regression is significantly less than unity ($t = -2.28$, 47 df, $P < 0.025$), confirming that younger females ovulated more frequently than older porpoises. Older females usually ovulated only once each year and became pregnant.

The estimated pregnancy rate was 0.86 (SD = 0.049) when the presence of a corpus luteum was used as the criterion of pregnancy (Table 1). When the presence of a foetus was used as the criterion of pregnancy and the sample restricted to the period after most implantation had occurred, the pregnancy rate was 0.74 (SD = 0.076) (Table 2). However, delineation of the period after which most implantation has occurred was arbitrary; during the early stages of this period, four females were examined that possessed corpora lutea but no foetus. If these four females were pregnant but sampled prior to implantation, the estimated pregnancy rate would be 0.86.

A high fecundity rate was also reflected by the proportion of mature females in the sample (0.54) that were lactating (Table 1). When primaparous individuals ($n = 9$) were excluded from the sample of mature females because they had just conceived for the first time and, therefore, could not possibly be lactating, the proportion of lactating females rose to 0.79.

Discussion

If sampling is random, mean age of first-time ovulators is an unbiased but imprecise estimate of age at sexual maturity (DeMaster 1984). The imprecision results from the small sample size of first-time ovulators that is usually available for study. The estimate of age at sexual maturity produced using the method of DeMaster (1978) is positively biased, because all age-classes are weighted evenly in the calculation, although older age-classes comprise less of the population than do younger classes (DeMaster 1984). The estimate of age at sexual maturity calculated using the latter method was slightly higher than mean age of first-time ovulators, although the difference was not statistically significant.

Estimates of mean age at sexual maturity have not been previously reported for any harbour porpoise population. Gaskin et al. (1984) noted that most female porpoises in the Bay of Fundy reached sexual maturity between the ages of three and four, in agreement with the results from this study. van Utrecht (1978) examined a small sample from the North Sea and asserted that female porpoises in that region reached sexual maturity at six yr of age. Both studies noted that maturity was attained at a length of approximately 150 cm, suggesting the existence of interpopulation variation in growth rate, sampling biases, or differences in age estimation techniques. Unfortunately, with the limited data presented by van Utrecht (1978), it is impossible to adequately assess these various propositions.

The pattern of elevated ovulation rate in young female harbour porpoises is common among odontocete cetaceans (Perrin and Reilly 1984) and may represent a response to low conception rates experienced immediately after attainment of sexual maturity. As noted by Brodie (1971), a large number of corpora albicantia does not necessarily signify a correspondingly large number of previous pregnancies, as many corpora arise from ovulations that do not result in pregnancy. In many mammalian species, female reproductive success initially increases with age, due to a variety of factors including physical maturation, experience, and social dominance (Clutton-Brock 1988). In this study, harbour porpoises exhibited no evidence of reproductive senescence or declining fertility with advancing age.

In contrast to the results presented here, Gaskin et al. (1984) were unable to demonstrate a significant relationship between corpora counts and estimated age. However, the two studies are not strictly comparable because Gaskin et al. (1984) did not include corpora lutea, but did include corpora atretica (which arise from the process of follicular atresia) in total corpora counts. The positive relationship between corpora counts and age in the present study indicates that corpora albicantia persist for most of the lifespan of this species, as they do in some other odontocetes (Perrin and Reilly 1984).

Most sexually mature female porpoises in the present sample were pregnant, particularly those in older age-classes. As pointed out above, previous estimates of the proportion of pregnant females have underestimated the true value by failing to account for the effects of reproductive seasonality. However, it is possible to reexamine the data of Gaskin et al. (1984) and estimate pregnancy rate using the methods described here. The pregnancy rate after implantation (using the presence of a foetus as the criterion of pregnancy) is 0.90 (9 of 10 mature females pregnant). The pregnancy rate of the entire sample, using the presence of a corpus luteum as the criterion of pregnancy, is 0.91 (21 of 23 mature females pregnant).

Both the present study and that of Gaskin et al. (1984) examined pregnancy rate very early in gestation, and it is possible that the actual birth rate is somewhat lower due to abortion and foetal resorption. The only study to examine harbour porpoise reproduction later in gestation was reported by Møhl-Hansen (1954), who obtained a large sample of mature females between November and February. It is not possible to estimate pregnancy rate directly from his sample, because no data on sexual maturity (other than the presence of a foetus) were presented. However, Møhl-Hansen (1954) noted that most females with a mass greater than 50 kg were sexually mature. Of 111 porpoises with mass greater than 50 kg in his sample, 93 were pregnant, yielding an approximate pregnancy rate of 0.84. It appears, therefore, that pregnancy rate does not decrease dramatically over the course of the year.

The findings presented here may have been influenced by several potential biases: errors in age estimation, selectivity of fishing gear towards certain age or reproductive classes, and segregation of age and reproductive classes leading to nonrandom sampling of females.

Although errors in age estimation undoubtedly add to variance in the estimation of age at sexual maturity, it is unlikely that such errors contribute any systematic bias. Most studies of age determination in harbour porpoises agree that longevity does not exceed 15 yr and that few individuals survive past 7 or 8 yr of age (Gaskin and Blair 1977; van Utrecht 1978; Stuart and Morejohn 1980; Noldus and de Klerk 1984; Watts and Gaskin 1989), even when different preparation techniques are used (Manzanilla 1987). There is general agreement that, at least for the first few years of life, a single growth layer group is deposited annually in the dentine (Nielsen 1972; International Whaling Commission 1980); thus, counts of dentinal growth layer groups correspond to actual age.

It is possible that certain age or reproductive classes are under-represented in the present sample because of nonrandom sampling of female porpoises by gill nets. For example, examination of the age distribution of the sample (Table 1) shows that calves are under-represented compared with older juveniles and young adult females. This may result from the inability of very young porpoises to dive to depths at which gill nets are set (Read and Gaskin 1988), from local segregation of mother-calf pairs (Smith and Gaskin 1983), or some combination of these factors. It is possible that the lack of calves in the sample is accompanied by an under-representation of lactating females, because of the strong association patterns of mothers and calves (Watson 1976). However, bias in the estimation of pregnancy rate will only occur if the pregnancy rate of these lactating females is different than that of females captured by gill nets, and this does not appear to be the case. The sample examined by Gaskin et al. (1984) was collected in an area where lactating females and calves are known to segregate, yet most of these females were pregnant (see above).

It is also possible that the sample is not representative of the population due to large-scale segregation of pregnant and nonpregnant female porpoises. For example, if nonpregnant females do not enter the Bay of Fundy during the summer, the high pregnancy rates observed in this study would over-estimate the true pregnancy rate of the population. However, both observational and theoretical evidence suggest that this is not the case. Watson (1976) observed two recognisable females that returned to the Bay of Fundy in successive years with new calves, and identified one individual three years in succession with a new calf each year. In a model of harbour porpoise population dynamics, Barlow (1986) assumed a realistic set of survival estimates and demonstrated that most adult females must give birth each year if positive population growth is to be achieved.

The observations reported here are indicative of annual reproduction in adult female harbour porpoises. The Dall's porpoise, *Phocoenoides dalli*, is the only other odontocete cetacean reported to exhibit annual reproduction (Newby 1982), although this pattern may prove to be common once more data is obtained from other small odontocetes. A high pregnancy rate is consistent with other aspects of the life history of the harbour porpoise: relatively short lifespan, litter size fixed at one, and a short lactation period. Even with a reproductive cycle of 1 yr, most female porpoises will not produce more than a few offspring during their lifetime.

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Variation in Agonistic Behavior between Newly Emerged Juveniles from Hatchery and Wild Populations of Coho Salmon, *Oncorhynchus kisutch*

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Swain, D. P., and B. E. Riddell. 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch*. Can. J. Fish. Aquat. Sci. 47: 566–571.

We compared agonistic behavior of newly emerged coho salmon (*Oncorhynchus kisutch*) between hatchery and wild populations using mirror image stimulation tests. We used hatchery populations from two different regions of Vancouver Island, B.C., each matched with a wild population from its region. In both comparisons, hatchery juveniles were more aggressive than wild juveniles. Rates of aggressive display increased with time since emergence for both hatchery and wild fish, as did the differences in behavior between the two types. By the sixth day of observation (13 d postemergence), the overall effect of fish type was highly significant for all aggressive behaviors. Since the individuals compared were reared from eggs under identical conditions, these differences are presumably genetic. Comparisons involved relatively few families from each population. However, because heritability was moderate to low within populations, and variance between population types exceeded variance among families within populations, these results indicate real differences at the population level. These results may have important implications for programs to rebuild wild populations using hatchery transplants and for selective breeding programs to develop domestic stocks of coho.

Nous avons comparé le comportement belliqueux de saumons cohos (*Oncorhynchus kisutch*) nouvellement émergés chez des populations sauvages et des populations d'élevage grâce à des tests de stimulation spéculaire. Nous avons utilisé des populations d'élevage provenant de deux régions différentes de l'île de Vancouver (C.-B.), chacune étant couplée à une population sauvage de la même région. Dans les deux tests, les juvéniles d'élevage se montraient plus agressifs que les juvéniles sauvages. Les manifestations agressives augmentaient en fonction du temps écoulé depuis l'émergence, pour les poissons sauvages et les autres, tout comme les différences de comportement entre ces deux types. Au sixième jour d'observation (13 jours après l'émergence), l'effet global du type de poisson était hautement significatif pour tous les comportements agressifs. Étant donné que les individus comparés provenaient d'oeufs incubés dans des conditions identiques, ces différences sont vraisemblablement d'origine génétique. Les comparaisons portaient sur un nombre relativement restreint de familles de chaque population. Toutefois, l'héritabilité étant modérée ou faible au sein des populations, et la variance entre les types de population dépassant la variance entre familles de la même population, ces résultats indiquent des différences réelles au niveau de la population. Ces résultats peuvent avoir des incidences importantes sur les programmes visant le rétablissement des populations sauvages à l'aide de stocks piscicoles transplantés et sur les programmes de reproduction sélective visant le développement de stocks indigènes de cohos.

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Salmonid fishes are cultured extensively in hatcheries to supplement natural production, and concerns about possible genetic effects of hatchery culture and interbreeding of hatchery and wild populations are widespread (e.g. Helle 1981; Larkin 1981; Ryman and Stahl 1981; Simon et al. 1986). Genetic divergence between hatchery populations and their wild progenors might be expected for two reasons. First, the use of small effective population sizes to initiate hatchery stocks may result in a loss of genetic variability and divergence from wild ancestors due to founder effect and genetic drift. Second, the novel hatchery environment may result in directional selection away from the wild type. Evidence is accumulating both for a loss of genetic variability in hatchery populations (Allendorf and Phelps 1980; Cross and King 1983; Vuorinen 1984; Vespoor 1988) and for genetic divergence between hatchery and wild populations in allozyme variation (Ryman and Stahl 1980) and in physiological, behavioral, and other performance traits related to fitness (Greene 1952; Vincent 1960; Flick and Webster 1964; Moyle 1969; Reisenbichler and McIntyre 1977; Bachman 1984).

Most of the evidence for divergence between hatchery and wild populations comes from the brook trout (*Salvelinus fontinalis*), which has been under intensive domestication for many generations (>100 yr), with broodstocks retained permanently at the hatchery site. In British Columbia, the coho salmon (*Oncorhynchus kisutch*) has been cultured in hatcheries only since the early 1970's. Only part of the life cycle is spent in

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the hatchery environment; juvenile coho are released from the hatchery usually about 1 yr after ponding, and broodstock is obtained from adults returning to the hatchery after 18 mo at sea. The extent of divergence between hatchery and wild populations in these circumstances is uncertain. Wild and hatchery coho do differ in morphology (Hjort and Schreck 1982; Taylor 1986; Fleming and Gross 1989), but this difference may be an environmental effect rather than a genetic difference (Taylor 1986).

In the wild, juvenile coho typically are territorial and display a variety of innate agonistic behaviors associated with territory defense (Chapman 1962; Mason and Chapman 1964; Hartman 1965). In hatcheries, juveniles are held at high densities and a territorial social structure is not evident. An analysis using game theory predicts that selection should favor unaggressive individuals in domestic environments (Doyle and Talbot 1986). However, in Atlantic salmon (*Salmo salar*), hatchery-reared parr are more aggressive than wild-caught parr at all but very low densities (Fenderson et al. 1968; Fenderson and Carpenter 1971). This difference is probably an environmental one, since the hatchery-reared parr were the progeny of wild parents. However, in brook trout, limited evidence suggests that there may also be a genetic effect towards greater aggressiveness in hatchery than in wild juveniles (Moyle 1969). In this study, we test for a genetic difference in agonistic behavior between hatchery and wild populations of coho salmon. To control for the effects of environment and social experience, we compare behavior among recently emerged juveniles, all reared from fertilization in the same environment and each isolated from other individuals at emergence.

Material and Methods

Study Populations

Hatchery fish were collected from the Robertson Creek and Big Qualicum Hatcheries on Vancouver Island, B.C. We tested juveniles of the 1987 brood, the descendants of five generations of hatchery culture in both cases. Each hatchery population was matched with a wild population from the same area. Robertson Creek Hatchery is on the Stamp River system on the west coast of Vancouver Island; hatchery fish were compared with wild fish from the Ash River, a major tributary entering the Stamp less than 5 km downstream of the hatchery. Big Qualicum hatchery fish were compared with Little Qualicum wild fish; both systems drain into the Strait of Georgia within 10 km of each other on the east coast of Vancouver Island. Because these wild populations may receive strays from the respective hatchery populations, our test for differences between wild and hatchery populations may be conservative.

Gametes from the Robertson Creek and Ash River populations (hereafter, the Stamp populations) were artificially crossed at the Pacific Biological Station, Nanaimo, to produce 10 Robertson Creek families (10 females × 10 males) and 13 Ash River families (four females and five males crossed as one pair, and a 3 × 4 set of factorial crosses). The difference in mating design between the two Stamp populations was necessary due to difficulties in obtaining ripe fish from the Ash River. Families were held in separate egg baskets and incubated at 6°C in the same stack of Heath trays. For tests of agonistic behavior, we randomly selected three individuals from each Robertson Creek family ($N = 30$) and two or three individuals from each Ash River family ($N = 27$). Fish from the Big and Little Qualicum populations (hereafter, the Qualicum populations) were incubated under similar conditions at the Big Qualicum Hatchery and were transported to Nanaimo when ready for ponding. About 30 fry were randomly selected from each of the two groups. The Big Qualicum group was derived from hatchery production crosses involving 191 females (×191 males), and the Little Qualicum group from 11 females (×11 males).

Mirror Image Stimulation

We quantified agonistic behavior using mirror image stimulation (MIS) tests (Gallup 1968). These tests have the advantage that individuals are tested against 'opponents' of exactly the same size and motivational state and that adequate replication is practical. Two behaviors are usually distinguished in MIS tests using salmonids: 'swim-against-mirror' (SAM) and 'lateral display.' SAM includes any swimming motion by a fish with its snout against the mirror (Rosenau 1984; Taylor and Larkin 1986), and is typically characterized by a violent shaking of the head and snapping of the jaws against the mirror. In lateral displays, fish orient parallel to the mirror with dorsal and anal fins erect and usually with pectoral fins lowered and mouth opened. We included 'wigwag' displays (i.e. lateral displays while swimming in an exaggerated motion with body stiffened) in this category. We defined total aggressive behavior as the sum of SAM and lateral display. We also distinguished 'submissive' displays, characterized by a fully depressed dorsal fin, a depressed anal fin, and often a folded caudal fin.

In juvenile coho and chinook salmon, reactions to mirror images are correlated with reactions to conspecifics (Rosenau 1984; Taylor and Larkin 1986; Rosenau and McPhail 1987; Taylor 1988; Swain and Holtby 1989). Populations that are more 'aggressive' in MIS tests (i.e. individuals spend more time in SAM and lateral display) are also more aggressive in stream tank tests of interactions among several individuals (i.e. individuals spend more time interacting with overt aggressive behaviors and lateral displays). Individuals from populations that are more aggressive in MIS tests also tend to dominate when paired with individuals from less aggressive populations (Rosenau and McPhail 1987). Thus, we believe that the results obtained here using MIS tests bear on the social interactions expected among individuals in more natural circumstances.

Test Procedure

Fry were removed from incubation trays and isolated in individual 14-L (30 × 20 × 23 cm deep) aquaria. (For convenience, this removal of fry from incubation trays is referred to here as 'emergence,' though we recognize that it may not correspond precisely to the time at which fry would naturally emerge from the gravel.) Each row of five or six aquaria was lit from behind by a 91 or 122 cm 40-W fluorescent bulb on a schedule of 16 h light: 8 h dark, and was fitted with an opaque plastic hood with observation slits 20 cm in front of each aquarium. Aquaria were opaque on three sides and contained gravel to a depth of 1–2 cm. Water was flowing in each aquarium and maintained temperatures at about 10°C. Fish were fed crushed Tetramin once daily, at least 3 h before testing. All fish had begun feeding before the start of the testing period. After 1 wk of acclimation, a mirror was placed in each aquarium once daily for seven consecutive days. After a 1-min period, durations of behavioral reactions were recorded with stopwatches for 3 min.

Statistical Analysis

Behavior durations were skewed strongly towards long bouts for some populations on some days. For each observation day, behavior durations were compared between hatchery and wild populations from a given region using Mann-Whitney U-tests. We also tested for an overall effect of population type (i.e. hatchery versus wild) on each observation day using an extension of the Kruskal-Wallis test to two-way ANOVA (Zar 1984, p. 219), with population type, region and their interaction as effects. To test for an effect of observation day, we used repeated measures ANOVA of rank-transformed data (Conover 1980), with population type and region as grouping factors and observation day as the repeated within-subjects factor. For each behavior, ranks were calculated over all days, regions, and population types.

These comparisons use the progeny of relatively small samples of parents from each population, particularly for the Stamp populations. We determined the amount of genetic variation for agonistic behavior within populations to assess whether these small samples were likely to be representative. If there was little genetic variation within populations, then the progeny from a small sample of parents would more likely be representative of the population. We addressed this question in three ways. First, for each of the Stamp populations, we calculated heritability using ANOVA of the rank-transformed averages of behavior durations on days 6 and 7 (the days when differences between population types were most significant). Heritability in the broad sense indicates the degree of genetic determination including all sources of genetic variation. Heritability in the narrow sense is the proportion of phenotypic variance that is due to additive genetic variation, and indicates the extent to which the phenotype is transmitted from parents to offspring. For the Robertson Creek population, estimates in the broad sense were derived from the full-sib intraclass correlation. For the Ash River population, heritability in the narrow sense was estimated from the sire variance component in a two-way cross-classified (4 sires × 3 dams) ANOVA of the rank-transformed data (see Becker 1984 for the causal components of variance in this design). Second, for all four populations, we calculated repeatability using data from observation days 6 and 7. Repeatability is the proportion of phenotypic variance that is due to permanent genetic and environmental differences among individuals (Falconer 1981). It sets an upper limit to heritability, though heritability may be much lower than repeatability. We calculated repeatability using ANOVA on rank-transformed data (with ranks calculated within populations and days). Third, for the Stamp stocks, we compared variance between population types to variance among full-sib families within populations using a nested ANOVA (families nested within populations types) of rank-transformed averages of the data on days 6 and 7.

Results

Behavior durations varied among observation days for all four behaviors ($P<0.001$). In general, behavior duration tended to increase over the observation period (Fig. 1). This could reflect ontogeny (i.e. learning or developmental stage) or acclimation to the test procedure. Because this effect is much less pronounced using older fry experienced in social interaction (Swain and Holtby 1989), it is presumably largely ontogenetic in this case.

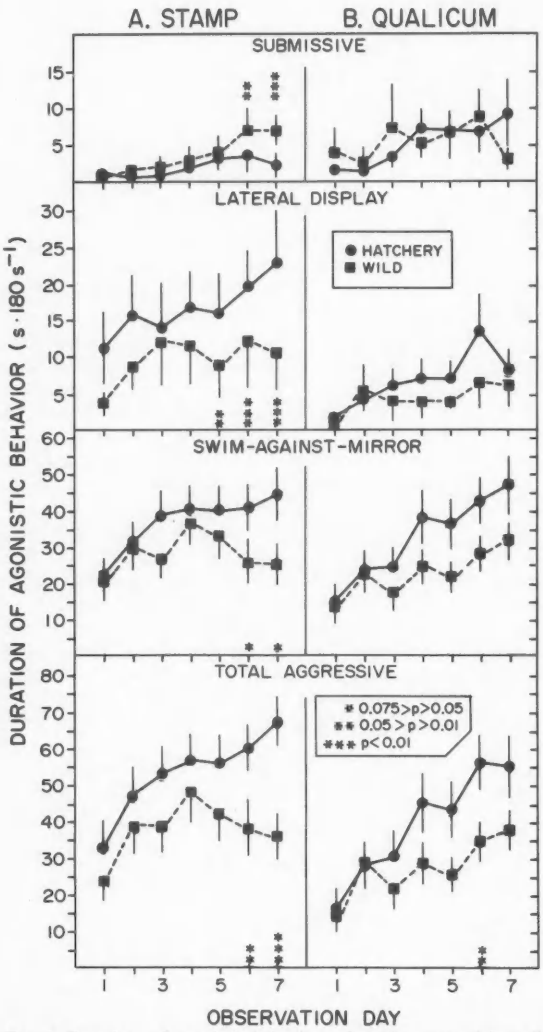

FIG. 1. Durations of agonistic behaviors of newly emerged juvenile coho salmon from hatchery and wild populations in mirror image stimulation tests. Total aggressive = swim against mirror + lateral display. Probabilities from Mann-Whitney U-tests. Vertical bars are standard errors of the means. Sample sizes on each day of observation are: Stamp hatchery, 30; Stamp wild, 27; Qualicum hatchery, 28; Qualicum wild, 30.

Durations of all aggressive behaviors tended to be greater in hatchery populations than in their respective wild populations. Differences in duration of aggressive behaviors between the two types tended to increase over the course of the experiment, from no difference on the first day of observation to significant differences on the sixth and seventh days of observation (Fig. 1). Although the hatchery population was more aggressive than the wild population in both regions, the difference was much stronger between the Stamp populations than between the Qualicum populations. Overall, the greater aggressiveness of hatchery populations compared with wild populations was highly significant on observation days 6 and 7 (13–14 d postemergence, Table 1).

TABLE 1. Overall significance of the effect of population type (hatchery versus wild) on agonistic behavior in mirror image stimulation tests. Probabilities are from two-way ANOVA on ranks with population type, region, and their interaction as effects.

	Observation Day						
Behavior	1	2	3	4	5	6	7
Total aggressive	0.3	0.9	0.1	0.2	0.06	0.001	0.002
Swim against mirror	0.5	0.7	0.1	0.4	0.1	0.02	0.02
Lateral display	0.1	0.8	0.2	0.08	0.1	0.002	0.01
Submissive display	0.4	0.6	0.5	0.9	0.9	0.3	0.3[a]

[a]significant ($P<0.05$) interaction between effects of population type and region.

TABLE 2. Repeatabilities of agonistic behaviors on observation days 6 and 7.

Population	*df*	Lateral display	Swim against mirror	Total aggressive	Submissive display
Robertson Creek	29,59	0.86[c]	0.49[b]	0.36[a]	0.24
Ash River	26,53	0.39[a]	0.63[c]	0.66[c]	0.23
Big Qualicum	27,55	0.50[b]	0.60[c]	0.69[c]	0.37[a]
Little Qualicum	29,59	0.44[b]	0.69[c]	0.71[c]	0.44[b]

[a] $0.05 > P > 0.01$.
[b] $0.01 > P > 0.001$.
[c] $P < 0.001$.

Hatchery and wild populations from the Qualicum region did not differ in duration of submissive display. However, in the Stamp region, the wild population showed a significantly greater duration of submissive display than did the hatchery population on days 6 and 7 (Fig. 1). This interaction between region and the effect of population type was significant on day 7 ($P<0.01$). The low duration of submissive display by Stamp hatchery fish did not appear to be simply the result of high levels of aggressive activity occupying most of the test period: the average duration of aggressive behavior was less than 40% of the test period on all days.

Repeatability was moderate to high, and was significant for all behaviors in all populations with the exception of submissive behavior in the Stamp populations (Table 2). However, repeatability apparently resulted mostly from permanent environmental differences among individuals, rather than from genetic differences. Family (Robertson Creek) and sire (Ash River) effects were nonsignificant in all cases ($P>0.1$), and point estimates of heritability were moderate to low (Table 3). In no case did heritability differ significantly from zero (Table 3). Thus, little genetic variation is apparent within populations, and the small samples of parents taken from the Stamp populations should be representative of those populations. Furthermore, for all four behaviors, the difference between the Stamp hatchery and wild populations significantly exceeded the differences among families within populations (total aggressive: $F_{1,21}=11.66$, $P<0.003$; SAM: $F_{1,21}=5.45$, $P<0.03$; lateral display: $F_{1,21}=11.25$, $P=0.003$; submissive display: $F_{1,21}=8.95$, $P=0.007$). These results suggest that the differences reported here indicate real differences between populations rather than chance differences between families sampled from similar populations.

Discussion

After a 4–5 d developmental or learning period, durations of mirror-elicited agonistic display were significantly greater among hatchery than among wild fish in our study. A possible explanation for this difference is that wild fish habituated to their mirror image over the 7-d test period. This possibility seems unlikely. Fish were exposed to their mirror image for only 4 out of 1440 min each day. In other experiments, we have exposed wild fish to their mirror image for several hours at a time and have detected no habituation in subsequent tests (D. P. Swain and L. B. Holtby, unpubl. observ.). Other studies have demonstrated a positive correlation among populations between the duration of mirror-elicited agonistic display and the level of aggressiveness among individual fish (Taylor and Larkin 1986; Rosenau and McPhail 1987; Taylor 1988; Swain and Holtby 1989). Thus, we conclude that our results indicate higher levels of aggressiveness in hatchery than in wild fish.

TABLE 3. Heritability (h^2) of agonistic behaviors in the Robertson Creek hatchery and Ash River wild populations. Heritabilities are in the broad sense for the Robertson Creek population and in the narrow sense for the Ash River population. Negative values should be interpreted as zero. SE = standard error.

	Robertson Creek		Ash River	
Behavior	h^2	SE	h^2	SE
Total aggressive	0.29	0.43	0.46	0.47
Swim-against-mirror	−0.15	0.35	0.25	0.48
Lateral display	−0.35	0.29	0.001	0.34
Submissive display	−0.28	0.32	−0.55	0.55

We tested fish that were reared from fertilization in the same environment. Thus, the difference in aggressiveness between hatchery and wild fish must have been due to a genetic difference between the two types or to prefertilization environmental differences (e.g. environmental maternal effects). A genetic basis has been demonstrated for behavioral differences among families (Bakker 1986), populations (Rosenau and McPhail 1987), and closely-related species of fishes (Ferguson and Noakes 1982, 1983), but we know of no studies indicating an effect of the prefertilization (e.g. maternal) environment on behavior. Therefore, the behavioral differences that we report between hatchery and wild populations are probably genetically determined.

The possibility that these results are explained by interpopulational differences unrelated to hatchery culture cannot be ruled out. Rosenau and McPhail (1987) have demonstrated genetic differences in agonistic behavior between wild populations of coho salmon. The two populations in their study were from streams that were separated by about 80 km and that differed greatly both physically and ecologically. They argued that the differences in agonistic behavior observed between populations were adaptations to these differences in local environments. In our study, the matched wild and hatchery populations were from similar streams (separated by about 10 km or less), so adaptive differences in agonistic behavior between the wild populations and the founding populations of hatchery stocks are less likely in this case. Furthermore, the consistency of our results between regions also supports the hypothesis that the differences we report are related to hatchery culture.

An adaptive basis can be suggested for the observed differences in aggressiveness between hatchery and wild populations. In the wild, increased aggressiveness may incur a cost through increased susceptibility to predation (cf. Rosenau and McPhail 1987). Freed from this cost in the hatchery environment, increased aggressiveness should be favored in hatchery juve-

niles if advantageous, or if juvenile aggressiveness is genetically correlated with some other advantageous trait, such as aggressiveness during the free-ranging marine stage (Paszkowski and Olla 1985). An advantage to aggressiveness in the hatchery environment seems plausible. More aggressive individual may enjoy faster growth (e.g. Jobling 1985; cf. Doyle and Talbot 1986), either by occupying more productive feeding stations or by modifying the 'appetite' (e.g. Koebele 1985) or food handling efficiency (Metcalfe 1989) of subordinates. Thus, aggressiveness may be positively correlated with body size at release from hatcheries, and with marine survival if mortality is inversely related to body size. An inverse relationship between mortality and body size has been suggested by several authors (e.g., Ricker 1962; Bilton et al. 1982; Healey 1982; Hargreaves and LeBrasseur 1986).

Our empirical results contrast with the theoretical predictions of Doyle and Talbot (1986). Using game theory, they argued that selection in domestic environments will favor unaggressive fish and cite the increased tameness of domestic brook trout (Vincent 1960) as empirical support for their hypothesis. However, a distinction must be made between aggressiveness and tameness or wariness. Although domestic brook trout are more tame than wild trout (i.e. they are less responsive to human disturbance), the evidence is that they are also more aggressive than their wild counterparts in interactions with conspecifics (Moyle 1969).

Juveniles from hatchery stocks are sometimes transplanted to the wild in an effort to rebuild wild production or utilize excess hatchery production. Our results could have serious implications for this practice. More aggressive hatchery juveniles may displace resident wild juveniles. Then, because of greater susceptibility to predation as a result of their higher rate of agnostic display or because of some other adaptive difference between hatchery and native fish, these hatchery juveniles may suffer higher mortality during freshwater residence than would have been experienced by resident fish. The result would be a decrease in production of resident wild fish, and possibly an eventual decrease in total production (e.g. Nickelson et al. 1986).

Our results may also have serious implications for selective breeding programs and the development of domestic stocks of coho for fish farming. A widespread concern among aquacultural geneticists is that, if growth is related to competitive ability, then selection for rapid growth will indirectly select for aggressiveness rather than for assimilative capacity or physiological growth rate (cf. Doyle and Talbot 1986). Because a genetic improvement in competitive ability (i.e. aggressiveness) results in an increase in the mean competitive ability of all contemporaries, such selection would not result in improved growth (e.g. Kinghorn 1983). Our results, and those of Moyle (1969), suggest that artificial culture may indeed lead to increased aggressiveness in salmon, perhaps as an indirect result of selection for rapid growth and large smolt size. These empirical results, in contrast to the theoretical predictions of Doyle and Talbot (1986), suggest that concern for a correlation between aggressiveness and growth rate in domestic environments may be well founded, and that the incorporation of behavioral criteria into selection programs may be important to their success.

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Transport and Storage of ^{137}Cs and ^{210}Pb in Sediments of Lake St. Clair[1]

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In 1985 cores were collected by diver from areas with fine-grained sediments in Lake St. Clair. Although the lake is shallow, rapidly flushed, and possesses only a thin layer of postglacial sediment (ca. 30 cm max.), 8% of the estimated ^{137}Cs loading from atmospheric nuclear testing in the mid-1960s and 13% of the potential standing crop of excess ^{210}Pb were retained. A sediment column transport model including eddy diffusive mixing, advection, and resuspension, acceptably described the vertical distribution of these radionuclides as well as stable lead and implied that such efficient retention may be of recent origin, occurring with the onset of net sedimentation about 100 yr ago. The model showed that, at selected sites, the history of lake loading by particle-associated contaminants can be reconstructed from sediment profiles. Horizontally averaged characteristics of the deposit indicate a surface mixed layer mass of 5 $g \cdot cm^{-2}$ and tracer residence time of 3 yr in accord with residence times of surficial Hg, PCBs, and DDT. Trap-collected materials from two sites show markedly contrasting seasonal variations in ^{137}Cs activity reflecting differing proportions of particles derived from inflow (ca 300 $mBq \cdot g^{-1}$) and resuspension (<30 $mBq \cdot g^{-1}$).

En 1985, des plongeurs ont recueilli des carottes dans des zones de sédiments à granulométrie fine du lac St-Clair. Bien que le lac soit peu profond, connaisse une vidange rapide et ne possède qu'une fine couche de sédiments post-glaciaires (env. 30 cm max.), 8 % de la charge estimée de ^{137}Cs provenant des essais nucléaires atmosphériques du milieu des années 60 et 13 % du stock potentiel de ^{210}Pb excédentaire s'y trouvaient retenus. Un modèle du transport des sédiments dans la colonne d'eau, qui tenait compte du mélange par diffusion turbulente, de l'advection et de la remise en suspension, décrivait de façon acceptable la répartition verticale de ces radionucléides ainsi que du plomb stable et semblait indiquer que cette rétention efficace pouvait être d'origine récente et remonter au début de la sédimentation nette, il y a environ 110 ans. Le modèle a montré que, en certains points, l'histoire de la charge du lac en polluants liés à des particules peut être reconstruite à partir des profils des sédiments. Après calcul de la moyenne horizontale, les caractéristiques du dépôt indiquent une masse de 5 $g \cdot cm^{-2}$ dans la couche mélangée de surface et un temps de résidence des traceurs de 3 ans qui concorde avec les temps de résidence de Hg, des BPC et des DDT en surface. Les matériaux collectés dans un piège en deux points montrent des variations saisonnières fortement contrastées dans l'activité du ^{137}Cs, ce qui reflète des proportions différentes des particules provenant de l'apport d'eau (env. 300 $mBq \cdot g^{-1}$) et de la remise en suspension (< 30 $mBq \cdot g^{-1}$).

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Lake St. Clair, situated between Lake Huron to the north and Lake Erie to the south, is a small (1114 km^2), shallow (3.6 m mean depth) water body in the chain of Great Lakes. Lake Huron waters enter the lake from the St. Clair River and leave via the Detroit River en route to Lake Erie. The intense urban and industrial activity along the shore of the St. Clair River has resulted in heavy contamination of biota, water, and sediments. Although the system is rapidly flushed (9-d mean hydraulic residence time) significant levels of particle-associated contaminants such as mercury (Thomas et al. 1977) and persistent chlorinated organic compounds (Frank et al. 1977) are retained in bottom sediments and found in resuspended materials (Pugsley et al. 1985; Oliver and Bourbonniere 1985; Oliver and Pugsley 1986; Charlton and Oliver 1986). Significant contamination persists in surface sediments declining only slowly over years to decades following reduction of loads (Thomas et al. 1977).

The fate of particle-associated tracers and contaminants in a shallow, energetic, and well-flushed lake such as St. Clair contrasts with the large deep lakes particularly because of the intense physical disruption, resuspension, and horizontal redistribution of surface sediments. Charlton and Oliver (1986) have

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reported resuspension mass fluxes over 600 $g \cdot m^{-2} \cdot d^{-1}$ which are up to 100 times the fluxes observed in offshore sites and about 20 times the fluxes at nearshore sites in Lake Ontario (Charlton 1983). Suspended fine-grained material entering the lake has such a short mean settling time (about 2 d) that essentially all material comes into contact with the sediment–water interface. Some fraction is incorporated into sediments while the rest is transferred either directly or following exchange processes, particularly resuspension, out of the lake through the Detroit River. The sedimentary load is subject to horizontal and vertical redistribution through a complex set of processes which include short-term sedimentation, mixing, resuspension, and possibly other forms of interfacial exhange. In Lake St. Clair recent (postglacial) sediments are shallow, possessing a mean depth of only 7 cm and a maximum depth of about 30 cm. For this reason the lake has been considered nondepositional (Thomas et al. 1977) having comparable sedimentation and resuspension mass fluxes averaged over some sufficiently long but unknown period of time. The mixing of surface sediments is undoubtedly a combination of continuous and event-related physical processes which includes the action of waves, seasonally varying currents, ice scouring in the littoral zone, and various human activities such as boating, fishing, shipping operations involving large vessels, dredging, and spoils dumping. In addition, biological mixing is likely since sediments host a range of active organisms including large Unionid clams and tube-dwelling *Hexagenia* larvae.

The sediment reservoir can be quantitatively characterized by determining the horizontal and vertical distributions and storage of particle-associated tracers whose loading histories as well as degradation pathways, in contrast to most contaminants, are well-known. Fallout ^{137}Cs ($t_{1/2}$ = 30.2 yr) is especially useful for this purpose since it is a tracer of fine-grained (clay sized) constituents, and has an accurately known input history and well-defined decay mode. A second isotope, ^{210}Pb ($t_{1/2}$ = 22.3 yr) is also of use, since it is delivered to the lakes at a virtually constant rate and has no significant anthropogenic sources. While ^{137}Cs illustrates the long-term response of sediments to a pulse of radioactivity passing through the system in the mid 1960s, ^{210}Pb characterizes the quasi steady-state response. These radionuclides have been employed successfully to determine the nature of sedimentation, focusing, and mixing processes, and their rates elsewhere in the Great Lakes (Robbins and Edgington 1975; Robbins et al. 1978; Robbins 1980; Eadie and Robbins 1987). It should be emphasized that in a dynamic, heavily-perturbed, ostensibly nondepositional system such as Lake St. Clair the conventional use of ^{210}Pb as a dating tool must not be taken for granted. In this paper we demonstrate that the two isotopes can produce consistent quantitative information on the extent of mixing, rates of sedimentation, residence times of particles in the sedimentary reservoir, and sources of suspended material.

Methods

Sediment cores were collected at the sites shown in Fig. 1a. during May and September 1985. The locations coincided with those occupied previously by Pugsley et al. (1985) where fine-grained sediments occurred. Sites with sand or coarser materials were not cored since such deposits were unsuited for hand insertion of core tubes and, at least for ^{137}Cs, possess insignificant amounts of the isotope (Robbins 1980). A 10.1-cm diameter core was collected by diver at each location (with no observed disturbance of the sediment–water interface), extruded hydraulically, and sectioned in 1-cm intervals to 10 cm and in 2-cm intervals from 10 cm to the bottom of the core or in many cases to an interface consisting of gray clay. Because the accuracy of sediment tracer and contaminant inventories depends on the extent of recovery of material from a known cross-sectional area, care was taken to collect all sediment (without trimming) from each section. We also analyzed 50 samples of the upper 2 cm of sediment collected by a Shipek grab sampler in 1976 at a regularly spaced network of sites with comparable spacing and coverage (Thomas et al. 1977).

In addition, sediment trap samples collected by Charlton and Oliver (1986) from two sites (T10, 6-m depth and T13, 4.5-m depth; Fig. 1a.) were analyzed for gamma-emitting radionuclides. Traps were placed at mid-water depths for nine (about equally spaced) time intervals during the period from early June to mid-November, 1985. Details of field methods and sample preparation are given in the above reference.

Core sections were weighed, freeze-dried, and reweighed to obtain the fractional dry weight (FDW) and the mass per unit area. Dried samples were lightly disaggregated and placed in vials of standard geometry for gamma counting. The activities of ^{137}Cs (661.6 KeV) and ^{40}K (1460.7 KeV) were determined using a lithium-drifted germanium detector coupled to a multichannel analyzer. The activity of ^{40}K ($t_{1/2} = 1.3 \times 10^9$ yr) is automatically determined with ^{137}Cs by the gamma counting method and is a measure of the total potassium content associated with nonquartz, primarily clay, minerals. Absolute detector efficiencies were established by counting sediment samples of equivalent geometry and weight spiked with a mixture of gamma-emitting radionuclides of known activity. Counting efficiency for ^{137}Cs was obtained by direct comparison with the ^{137}Cs activity of the spike. For ^{40}K the efficiency was determined by interpolation using an efficiency-energy relation (for a specified sample weight) described by a third-order polynomial with least-squares optimized coefficients. Uncertainties in sample activities were generally well under 10% for ^{137}Cs and about 15% for ^{40}K.

The ^{210}Pb activity was determined by analysis of its alpha emitting daughter product, ^{210}Po ($t_{1/2}$ = 138.4 d). Because its short half-life, ^{210}Po is generally in secular equilibrium with its parent under in situ conditions. Secular equilibrium was promoted additionally by storing isolated core sections for roughly two half-lives of ^{210}Po prior to extraction. A 5-g sample of dry sediment from each section plus 1 mL of spike of ^{209}Po ($t_{1/2}$ = 100 yr) were placed in 50 mL 50% (v/v) HCl at 85°C for 8 h. Periodically, small (5 mL) amounts of 30% H_2O_2 were added to oxidize organic matter. Following extraction, the mixture was filtered (0.45 microns) and the residue dried and weighted to obtain the fraction soluble (FSOL = weight of sediment extracted / total dry weight). Two grams of $NH_2OH \cdot HCl$ were added to the filtrate to remove the interference of dissolved iron with polonium plating (Flynn 1968) and the solution was brought to 50 mL by addition of distilled water, and adjusted to pH of 1.5 via small additions of concentrated NH_4OH. The two polonium isotopes were self-plated onto a polished, mylar tape-backed copper disk placed in the solution (at 85°C) and gently agitated for 8 h. Active disks were counted by alpha spectroscopy using a surface barrier detector coupled to a multichannel analyzer. Activities of ^{210}Po were calculated from the ratio of its counting rate to that of ^{209}Po and the precisely known activity of the spike (122 ± 1 dpm/mL) based on an intercalibration with a National Bureau of Standards ^{208}Po solution.

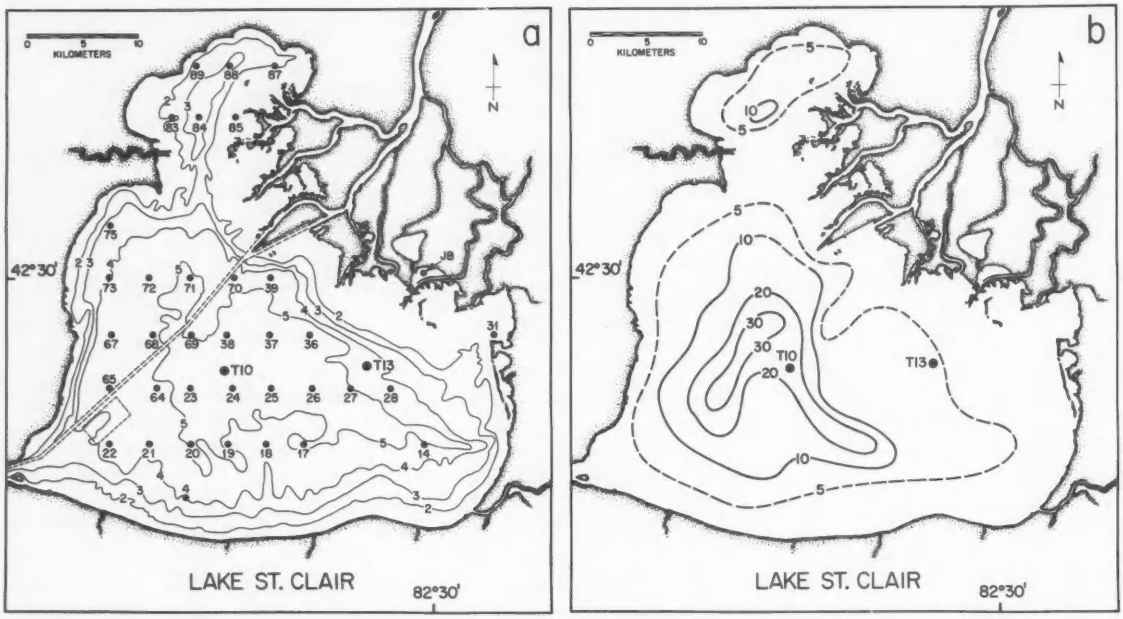

FIG. 1. (a) Locations of the 1985 coring sites in Lake St. Clair. Stations correspond to those occupied previously in the University of Windsor study (Pugsley et al. 1985). Depth contours in metres. Also shown are trap deployment sites T10 and T13. (b) Thickness (cm) of recent sediments overlying postglacial clay.

This tracer addition method eliminates uncertainties in chemical yields and counter efficiencies. Analytical uncertainties in ^{210}Pb activity were generally well under 10%.

To estimate the affinity of ^{137}Cs for sediment particles, 10 g (equivalent dry weight) portions of surface sediment (upper 10 cm combined from a series of cores) were digested in (I) 50 mL of 10% HCl (v/v) at ca. 20°C, (II) 50 mL 50% HCl (v/v) with additions of 30% H_2O_2 (total of 10 mL) at ca. 20°C, and in (III) 50 mL hot (initially boiling) aqua regia. In each case sediments were extracted for 3 d, then centrifuged and the residue analyzed for ^{137}Cs and ^{40}K.

Results and Discussion

Radionuclide Loadings to Lake St. Clair

Quantitative treatment of the transport and storage of radiotracers in the sediment reservoir requires an accurate estimate of radionuclide loadings to the lake. In the Great Lakes ^{137}Cs has originated almost exclusively from atmospheric nuclear testing occurring mainly in the mid 1960s. There are no natural sources of the radionuclide and contributions from reactors situated along the shores are many orders of magnitude less than fallout. Routine monitoring of monthly deposition, supplemented by atmospheric activity measurements during the past 30 yr by United States and Canadian agencies, has generated a data base which greatly surpasses, both in quantity and quality, that of any other contaminant. Data for ^{137}Cs (and ^{90}Sr which correlates strongly with ^{137}Cs) from all monitoring sites in the Great Lakes region have been combined with concentration-deposition rate models to estimate monthly atmospheric loadings to each of the lakes and their drainage basins (Robbins 1985a). The loading data were in turn used to

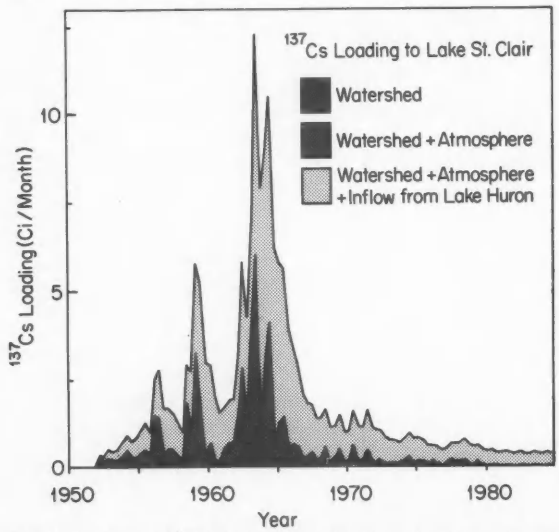

FIG. 2. Loadings of ^{137}Cs to Lake St. Clair from the three principal sources: inflow from Lake Huron, direct fallout and transfer from the drainage basin (1 Ci = 37 GBq).

estimate monthly mean lake water concentrations using a coupled lakes model, CLM (Robbins 1985b), which is a comprehensive version of existing models treating the lakes as an interconnected system of well-mixed reactors (Lerman and Taniguchi 1972; Wahlgren et al. 1980; Thomann and DiToro 1983). The few free model parameters were adjusted to best describe measured ^{137}Cs activities in each of the five major

lakes. Because the residence time of ^{137}Cs is short (a few years) the only lake contributing significant amounts of ^{137}Cs to Lake St. Clair is Huron. Uncertainties in model loads from the upper lakes (Superior and Michigan) have a negligible effect on estimates of activities in St. Clair. Moreover, since the most comprehensive set of measured activities of ^{137}Cs exist for Lake Huron (Barry 1973; Dasgupta 1975; Durham and Jamro 1981; Alberts and Wahlgren 1981) the model calibration for this lake has minimal uncertainty. Thus the estimate of loadings to Lake St. Clair through inflow are only weakly dependent on the assumptions of CLM.

The calibrated CLM calculation (Fig. 2) indicates that contributions from the watershed have been a small (less than 5%) virtually constant fraction of the loading. Direct atmospheric input was initially about 40% of the total load but decreased by 1980 to less than 20%. Inflow from Lake Huron has contributed the largest portion of the loading: about 60% during the period of maximum fallout increasing to more than 80% beyond 1980. This increase reflects the persistence of small amounts of the ^{137}Cs in Lake Huron water resulting from sediment–water exchange (resuspension). As of 1985 the total, decay-corrected loading to Lake St. Clair was estimated to be 17.39 TBq (470 Ci).

The accuracy of this load estimate depends on whether the CLM model correctly represents the activity in water exiting from Lake Huron. The CLM model is calibrated on ^{137}Cs activities measured under isothermal conditions (Barry 1973; Alberts and Wahlgren 1981; Tracy and Prantl 1983). Although the values reported by Alberts and Wahlgren (1981) for Lake Huron show no significant difference between surface and deep waters during the summer of 1976, ^{137}Cs is seasonally depleted in the epilimnion of Lake Michigan due to the sinking of components resuspended earlier during isothermal mixing. Such cycling should also occur in Huron so that surface waters which presumably exit preferentially from the lake could contribute less to Lake St. Clair during the summer months than predicted by the model. The calculation also assumes that the river system conveying the radionuclide to the lake has no significant sinks. This is probably true for the main section of the St. Clair river which has a coarse-grained, scoured bottom. The delta and marshy areas may plausibly store ^{137}Cs although deltaic deposits are coarse, sand-sized materials which possess little affinity for radionuclides. Finer grained materials accumulate in the open lake beyond the delta area (Thomas et al. 1977) although some fines are undoubtedly occluded with coarser materials in the regions of the delta. The marshy areas may trap fines efficiently but the proportion of water which flows through them is very small in comparison with open channel flow.

Although the above considerations also apply to loadings of ^{210}Pb, other uncertainties are undoubtedly greater. ^{210}Pb is formed in the atmosphere as the result of radon decay and enters the lake primarily through wet and dry deposition processes. Small contributions originate from watershed transfer and from in situ decay of parent nuclides. There are no reported measurements of ^{210}Pb deposition rates to the lakes. Atmospheric ^{210}Pb activities at Crystal Lake, Wisconsin (Talbot and Andren 1983) and at Argonne National Laboratory (D. Nelsen, pers. comm.) when combined with a radionuclide deposition model (Robbins 1985a) yielded mean rates of 1.6 and 1.4 $dpm \cdot cm^{-2} \cdot yr^{-1}$, respectively. Using a mean rate of 1.5 $dpm \cdot cm^{-2} \cdot yr^{-1}$ and distribution coefficient of 1×10^6 $mL \cdot g^{-1}$ (Eadie and Robbins 1987) we estimate (using CLM) the mean activity of ^{210}Pb in Lake Huron water to be 0.15 $dpm \cdot L^{-1}$. There are no reported measurements of ^{210}Pb in Lake Huron waters. Mean activities in Lake Michigan hypolimnetic waters are around 0.1 $dpm \cdot L^{-1}$ (L. Hugel, pers. comm.). In that lake, distribution coefficients vary seasonally in surface waters from about 3×10^5 $mL \cdot g^{-1}$ during isothermal conditions to 3×10^6 $mL \cdot g^{-1}$ during calcite precipitation (Eadie and Robbins 1987). The CLM calculation was thus consistent with the Lake Michigan data yielding a mean loading from inflow of about 370 $GBq \cdot yr^{-1}$, or 2 $dpm \cdot cm^{-2}$ of Lake St. Clair surface area per year. The atmospheric and inflow loadings are therefore comparable and total about 666 $GBq \cdot yr^{-1}$ or 3.5 $dpm \cdot cm^{-2} \cdot yr^{-1}$.

Characteristics of Sediment Cores

About the top centimetre of sediment in all cores consisted of gelatinous, flocculent material. The surfaces of many cores, particularly of sediments in the deepest parts of the lake, were perforated by circular holes about 0.5 cm in diameter numbering up to 400 hole pairs$\cdot m^{-2}$ (characteristic of *Hexagenia* larvae burrows). The holes in deeper sediments, when exposed by breaking friable material apart, were surrounded by about a 2 cm diameter "halo" of lighter brown ("oxidized") sediment contrasting with adjacent gray material, and were often inhabited by live *Hexagenia* larvae. Active burrows were occasionally observed as deep as 16 cm. In regions of the lake with high clay content, the upper 10–20 cm of sediments consisted of gray clayey silt with some fine sand and occasional layers of shell fragments. In a few of the cores stratigraphic inhomogenieties were observed as a layer a few centimetres thick between 10 and 20 cm, consisting of clay with high water content. Below this layer a mixture of clay and fine sand occurred which became more consolidated and increased in sand content with depth. In nearly all cores the sediment composition shifted abruptly to fine clay at depths corresponding roughly to lake bathymetry. The horizontal distribution of this depth (Fig. 1b) is consistent in magnitude as well as form with that previously reported by Thomas et al. (1977) as the thickness of postglacial sediments. Cores with low clay content collected in shallower parts of the lake occasionally possessed fragments of rooted plants (macrophytes). A large live clam, about 5 cm in length (Unionid), was found in the region of 2 to 6 cm depth in a sediment core (discarded) collected at site 39.

Vertical Distributions of ^{137}Cs

Representative profiles of ^{137}Cs are shown in Fig. 3 for sites along a transect between stations 65 and 28 (see Fig. 1a). Activities are generally low in comparison with surface sediments in Lake Huron or Lake Erie where values are typically around 20 $dpm \cdot g^{-1}$ and 5–10 $dpm \cdot g^{-1}$, respectively. In most cases maximum activity occurs 2 to 10 cm below the sediment surface. The extent of penetration of ^{137}Cs is generally shallow, ranging from 2–4 cm toward the ends of the transect to a maximum of about 14 cm around the transect midpoint. The occurrence of subsurface maxima suggests that some information about the loading time-dependence may be preserved in these deposits although its correspondence with profile shape is generally weak.

Profiles of ^{137}Cs at sites 69 and 38 have the best defined maxima of any from this lake. Both cores possess high values of ^{137}Cs at about 10 cm with secondary maxima at about 25 and 15 cm at sites 69 and 38, respectively (Fig. 4, top panels).

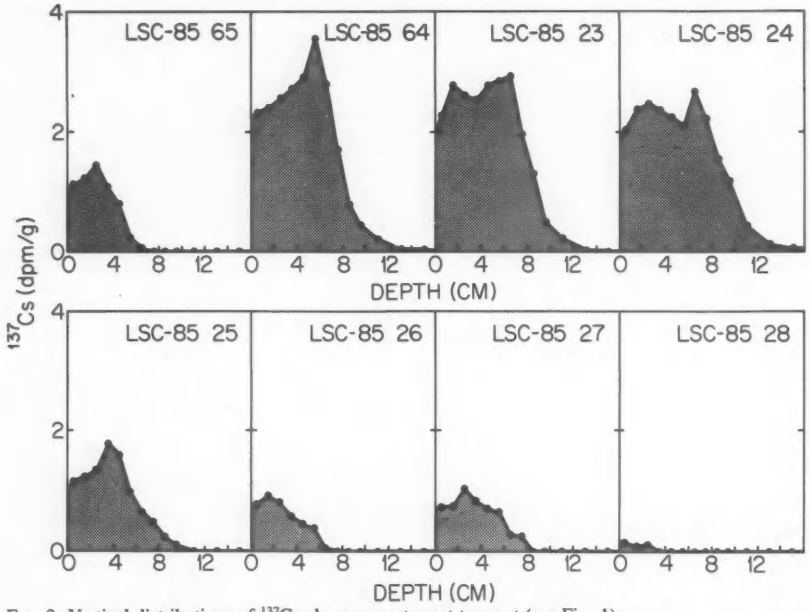

FIG. 3. Vertical distributions of ^{137}Cs along an east–west transect (see Fig. 1).

Despite the sharp profile structure, the correspondence with ^{137}Cs loading (dashed line) is poor. (Sedimentation rates have been chosen to arbitrarily place the peak loading at the position of maximum activity.) The secondary maximum is not reproduced nor are activities elsewhere outside of the peak region. The valley in the ^{137}Cs distribution (about 12 cm in 38 and 15 cm in 69) is associated with (1) a decrease in the sediment solids content (FDW) as verified both by field observation and measurement in both cores, (2) a small increase in the acid soluble fraction (FSOL) in core 69, and (3) a marked increase in the ^{40}K content over an interval of a few centimetres in both cores. The discontinuities in these cores of total potassium (^{40}K) indicates the interlaying of fine-grained (clay) materials of relatively high water content. As these two sites are relatively near the shipping channel (Fig. 1a) it is plausible the such layers as well as the material comprising the secondary peaks could originate from dredging operations. The only other core with an indication of double ^{137}Cs peaks from site 71 (Fig. 5) is also adjacent to the channel. Cores at adjacent sites 65, 68, and 70 do not have double peaks but in these cores the radionuclide may not penetrate sufficiently to reveal such stratigraphic anomalies.

Vertical Distributions of ^{210}Pb

Distributions of excess ^{210}Pb (Fig. 5) are computed by subtracting the activity of background ^{210}Pb originating from in situ radium decay. Background ^{210}Pb is taken as the average minimum activity in these cores: 1.0 ± 0.2 dpm·g^{-2}. In core 38 the total ^{210}Pb distribution is discontinuous: above 12 cm the activity is nearly uniform, averaging 4.6 ± 0.5 dpm·g^{-1} and below 12 cm it is also quite uniform averaging 1.9 ± 0.3 dpm·g^{-1}. In core 69, excess ^{210}Pb occurs down to the postglacial interface and shows major disturbances particularly in the vicinity of the stratigraphic anomaly around 15 cm. Excess ^{210}Pb in core 65 shows a region of nearly constant activity from about 5 to 10 cm which is accompanied by a lower FDW, elevated FSOL, and an increase in ^{40}K. In the other cores the ^{40}K content is uniform down to postglacial sediments indicating that distributions of ^{210}Pb as well as other contaminants are probably not stratigraphic artifacts. In these "stratigraphically normal" (SN) cores, excess ^{210}Pb distributions are essentially constant over a zone of variable thickness at the surface and decrease more or less exponentially below this zone. Such distributions are typical of those found in the Great Lakes, both in the open lake environment (Robbins and Edgington 1975; Robbins et al. 1978; Robbins 1980) and in the silty, shallower recent deposits of lower Saginaw Bay (Robbins 1986b).

Theoretical Treatment of Radionuclide Profiles

Mathematical models of tracer transport and diagenesis have been developed to treat many significant processes including compaction, sedimentation, eddy diffusive particle mixing (Goldberg and Koide 1962; Bruland 1974; Robbins 1978), diffusion, and reversible exchange between solids and pore water (Berner 1980), nonlocal (Boudreau 1986) and particle-selective (Robbins 1986a) transport, and variable sedimentation rates (Schelske et al. 1988). With few exceptions, such models assume continuous, although possibly time-varying transport processes. Event-related processes such as those possibly causing discontinuous tracer distributions in sediments near the shipping channel are not amenable to continuous models. Here it is assumed that transport in SN cores occurs as the result of continuous processes of net sedimentation (advection) and diffusive particle mixing represented by suitably time-averaged constant rates. Tracer distributions are then described by the equation,

$$(1) \quad dA/dt = d(K_b dA/dz)dz - w\,(dA/dz) - \lambda A,$$

where K_b is the depth-dependent coefficient for eddy-diffusive particle mixing (cm^2·yr^{-1}), w is the net sedimentation rate

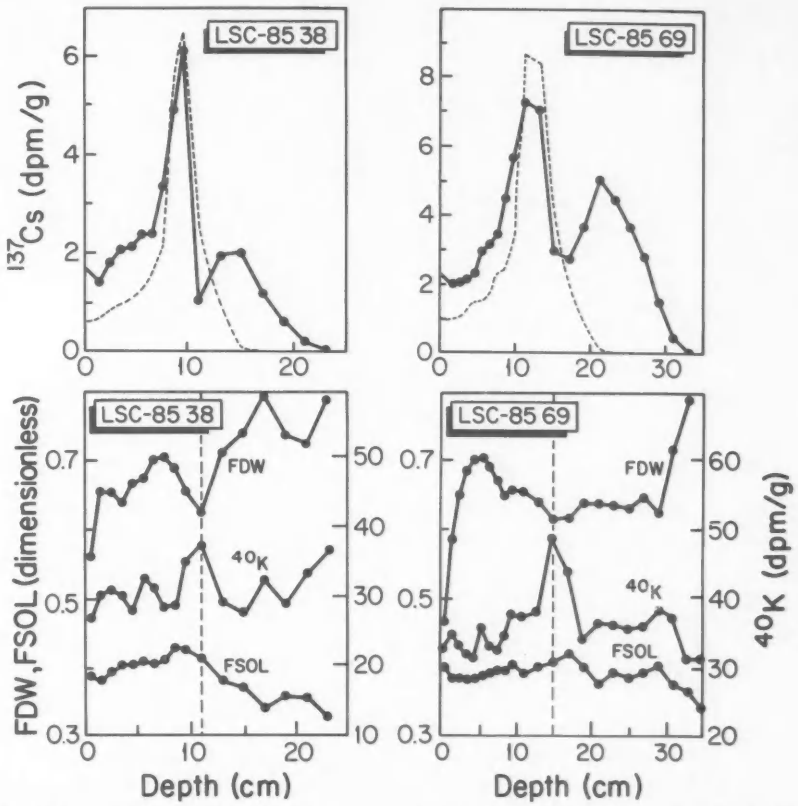

FIG. 4. (top panels) ^{137}Cs distributions in two cores with distinctive stratigraphic anomalies. The dashed line is the profile expected from direct transfer of cesium to undisturbed sediments with peak positions arbitrarily set. (lower panels) Distributions of quantities (see text) indicating bulk sediment composition.

(cm·yr^{-1}), and λ (yr^{-1}) is the radioactive decay constant ($=0.6932 / t_{1/2}$). By ignoring the small effect of sediment compaction and assuming a constant solids content, the activity A can be expressed in disintegrations per minute per gram. Two special cases of equation (1) are used below to interpret the data: a discreet layer representation of the mixing process which corresponds to previously published models and a model with continuous depth-dependent mixing and resuspension.

The total flux to the sediment surface, $F(t)$, is either proportional to the ^{137}Cs loading or constant in the case of ^{210}Pb. At the sediment–water interface ($z=0$) mass conservation requires that,

$$(2) \quad F(t) = v_r A - K_b dA/dz + wA,$$

where the first term is the flux from the sediments due to resuspension and v_r is the resuspension rate (cm·yr^{-1}). The remaining two terms are the downward fluxes due to eddy diffusive mixing and advection, respectively. The model treats resuspension as a continuous process which does not significantly disrupt the interface. The amount of sediment required to produce the observed amount of total suspended matter (TSM) is extremely small. Bukata et al. (1987) measured TSM values ranging from 2.5 to 16 mg·L^{-1} on transects across the lake in September 1985. Using the maximum value of about 20 mg·L^{-1}, the vertically integrated maximum TSM would be about 0.008 g·cm^{-2} for a mean lake depth of 4m. If this amount were due solely to resuspension the mean thickness of sediment resuspended would be only 0.03 cm. We have assumed that interfacial sediments have a mean porosity of 0.9 and a solids density of 2.5 g·cm^{-3}. Thus the average extent of involvement of the sediment column in the resuspension process is far smaller than profile scale lengths of 5 to 20 cm. Even episodes of intense resuspension may have a small effect on the interface at least in deeper regions of the lake. During storm events wave action in the lake, Skafel and Donelan (1989) observed brief escalations of TSM to values of perhaps as much as 200 mg·L^{-1}. Such events would resuspend, on average, 3 mm of sediment.

The above equations implicitly assume that molecular scale diffusion in sediments is insignificant. This assumption, while not valid for many aquatic systems, especially for ^{137}Cs, has been shown to be met in the Great Lakes environment based on direct studies of ^{137}Cs migration in sediments (Robbins et al. 1979), the affinity of these radionuclides for particulate matter (Alberts and Whalgren 1981; Robbins 1985b; Eadie and Robbins 1987) and the consistency between ^{210}Pb, ^{137}Cs and other measures of sedimentation rates (Robbins et al. 1978). The present selective extraction results also indicate the strong binding of radiocesium to particles. Three days of extraction in 10% HCl (I) left 98% of the isotope in the residual fraction

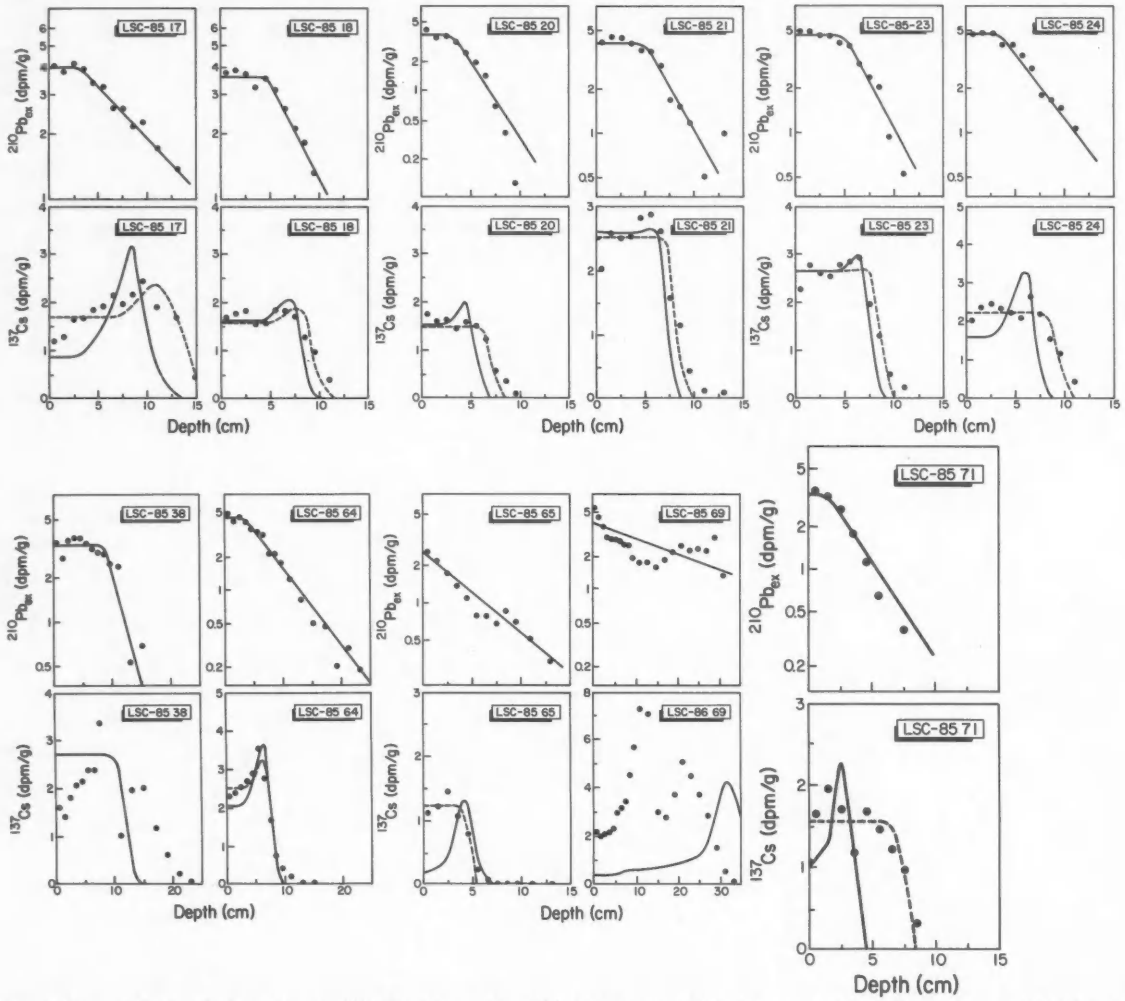

FIG. 5. (top panels) Distributions of excess ^{210}Pb (top, log scale) and ^{137}Cs (bottom panels) for 11 cores. Solid and dashed lines are RSSM model distributions.

TABLE 1. Extractability of ^{137}Cs and ^{40}K from a surface sediment composite sample (upper 5 cm.)

Treatment	Percent remaining with solids		
	$^{137}Cs^a$	$^{40}K^a$	$^{137}Cs^b$
I. 10% HCl	98	95	103
II. 50% HCl ($+H_2O_2$)	88	91	97
III. Aqua Regia	51	85	60

[a]Uncertainties are ±5%.
[b]Percent relative to ^{40}K.

(Table 1). The 50% HCl (II) treatment left nearly 90% unextracted. Even a 3-d exposure to hot aqua regia (III) removed only about 50% of the activity. As expected, ^{40}K was even more resistant to extraction. Eighty-five percent remained in the residual fraction after aqua regia treatment. The results are consistent with more conventional selective chemical extraction methods which showed that greater than 90% of ^{137}Cs is in the "fusion fraction" (residual mineral fraction) of sediments from Lake Michigan (Alberts et al. 1974 and 1989).

The Rapid Steady-State Mixing Model (RSSM)

The RSSM model used previously to interpret ^{210}Pb and ^{137}Cs distributions in sediments of the Great Lakes and elsewhere, is discussed in detail by Robbins et al. (1977). We have used this model as a primary interpretive tool because extensive programs have been developed to extract weighted least-squares sedimentation rates and other ancillary information from radiotracer distributions. The model corresponds to a special case of equation (1) in which intense particle mixing ($K_b = \infty$) occurs within a zone of well-defined thickness (mixed depth), s (cm), at the sediment–water interface (region 1: $z < s$). Below this zone (region 2: $z > s$) there is no mixing ($K_b = 0$). In this model there is no resuspension from the mixed layer ($v_r = 0$). Below

TABLE 2. Optimized RSSM model parameters based on excess ^{210}Pb distributions and storage of ^{137}Cs and excess ^{210}Pb.

Site	Mixed depth (cm)	Sedimentation rate[a] (cm·yr^{-1})	Total[b] ^{210}Pb (dpm·cm^{-2})	Total ^{137}Cs (dpm·cm^{-2})	^{137}Cs/^{210}Pb ratio
17	2,8	0.32	41.6	24.6	0.59
18	4.8	0.16	37.8	18.8	0.50
20	3.0	0.12	32.7	14.5	0.44
21	5.1	0.12	42.1	23.5	0.56
23	5.0	0.16	43.9	22.9	0.52
24	2.8	0.21	42.9	23.3	0.54
38	9.	0.16	61.6	50.8	0.83
64	3.1	0.20	55.3	22.7	0.41
65	<0.2	0.23	30.8	8.9	0.29
69	—	—	95.0	117.	1.2
71	1.2	0.10	24.4	19.0	0.78
Mean[c]	3.8	0.21	40.	20.	0.51
SD	1.1	0.08	9.	6.	0.06

[a]Sedimentation rates (w) are based on a supported lead-210 activity of 1.0 ± 0.2 dpm·g^{-1} and are average values over intervals with significant excess ^{210}Pb.

[b]Vertically integrated excess ^{210}Pb (storage).

[c]Excludes values in cores 38, 65, 69, and 71.

we use a less restrictive model to evaluate the accuracy of the RSSM model.

The solid lines shown in Fig. 5 (upper panels) are RSSM model results for excess ^{210}Pb in which values for w and s were chosen to yield the best weighted least-squares fit to the data. The agreement is reasonable except for the previously discussed cores 38 and 69. Apart from these cores (and 65) mixed depths have a relatively narrow range, averaging about 3.8 (±1.1) cm. Core 65 has no evident mixed zone. The mean (apparent) sedimentation rate is 0.21 (±0.08) cm·yr^{-1}. The RSSM model ^{137}Cs distributions shown as the solid lines in Fig. 5 (lower panels) are based on ^{210}Pb fit values of w and s. The only free parameter in this calculation was the total ^{137}Cs stored. In several cores, ordered by increasing standard deviation in the fit (18, 21, 64, 23, 20) the agreement between measured and predicted values is reasonable. Where there are small discrepancies, the ^{210}Pb based parameters predict more structure (sharper peak) in ^{137}Cs than is observed. This trend continues in two cores (24, 17) where the actual distributions are considerably broader. Another group of cores (71, 65, 38, 69) shows distinctly poorer agreement. The result of optimizing w and s for ^{137}Cs independently (dashed lines in Fig. 5) leads to generally greater mixed depths for ^{137}Cs than for ^{210}Pb at the sites. Sites (18. . .20) and (24, 17) cluster in the southern part of the lake and, except for 64, are remote from the shipping channel. The remaining sites (71. . .69) with inconsistent radionuclide profiles, cluster along the channel.

In the case of core 65, considerable mixing is implied by the ^{137}Cs data and no mixing by the ^{210}Pb data. This could occur if surface material was lost prior to or during coring. Surface sediment loss is consistent with ratios of total ^{137}Cs to total excess ^{210}Pb (Table 2). Three anomalous cores (38, 69, and 71) have ratios of 0.8–1.2. The remaining cores have ratios ranging from 0.4 to 0.6 while core 65 has a ratio of 0.29. Loss of surface sediment would reduce total ^{137}Cs in preference to excess ^{210}Pb.

While the RSSM model attributes the nearly exponential decrease in excess ^{210}Pb below the mixed zone to radioactive decay and advection only, the general solution of equation (1) allows for a linear combination of advective and diffusive transport if K_b is constant for $z > s$. The steady-state solution ($dA/dt = 0$) of equation (1) for ^{210}Pb below the mixed zone has the form,

$$(3)\quad A(z) = A_s e^{-\beta z},$$

where β is the experimentally determined slope of the log excess ^{210}Pb profile obtained above (RSSM model). Substituting this relation in equation (1) we obtain,

$$(4)\quad K_b\beta^2 + w\beta - \lambda = 0,$$

which has the solution

$$(5)\quad K_b(\infty) = (\lambda - w\beta)/\beta^2.$$

Thus all combinations of $K_b(\infty)$ and w satisfying equation (5) such that $0 < w < \lambda/\beta$, will give equivalent ^{210}Pb profiles. For the case of exclusively diffusive mixing ($w = 0$), $K_b(\infty)$ is given by λ/β^2. Robbins et al. (1978) used this limiting case to reconcile distributions of ^{137}Cs, ^{210}Pb, and pollen species in sediment cores from the shallow, perturbed sediments of western Lake Erie.

Continuous Transport and Resuspension Model (CTR)

To infer the "correct" combination of $K_b(\infty)$ and w, we searched for solutions of equation (1) which would best describe the ^{137}Cs distribution. For these calculations we introduced a continuous version of the RSSM model (CTR) in which the depth-dependence of K_b is given by:

$$(6)\quad K_b(z) = K_b(0) + (K_b(\infty) - K_b(0))g(z)$$

where

$$(7)\quad g(z) = \frac{1}{\sigma\sqrt{2\pi}} \int_0^z e^{-(u-s)^2/2\sigma^2}\, du$$

with $g(0) = 0$ and $g(\infty) = 1$.

The use of this particular form for the depth dependence of eddy-diffusive mixing coefficient introduces the variable σ, which allows for the realistic, gradual reduction of K_b with depth and avoids the necessity for boundary condition matching in computer-based numerical solution schemes. This form becomes equivalent to the RSSM model as $K_b(0) \to \infty$, $\sigma \to 0$, and $K_b(\infty) = 0$.

To calculate distributions of excess ^{210}Pb, equation (1) was solved by explicit methods for time-dependent differential equations (Crank 1975). The calculation was run for sufficiently long time periods to achieve a steady-state distribution over 30 cm of sediment. For each of eight SN cores the effective surface mixing rate constant and range, s, were determined by least-squares optimization with the RSSM-determined value of w and the value of σ fixed at 1 cm. All profiles were consistent with a value of $K_b(0) = 10$ cm^2·yr^{-1} and a range s which was generally about 1 cm less than corresponding RSSM model values because of the introduction of σ. The resulting depth-dependent $K_b(z)$ for sites 17 and 64 are shown in Fig. 6 for both ends of the allowed range in w. For site 17 parameter values for the fully advective case (a) are $K_b(\infty) = 0$ cm^2·yr^{-1} and $w = 0.32$ cm·yr^{-1}, and for the fully diffusive case (b) are $K_b(\infty) = 3.3$ cm^2·yr^{-1} and $w = 0$ cm·yr^{-1}. The resultant profiles (Fig. 7 upper panels) for these sites show that choices (a) and (b) are experimentally indistinguishable.

The choices (a) and (b) make a profound difference in the distribution of ^{137}Cs however. For core 17 the fully advective

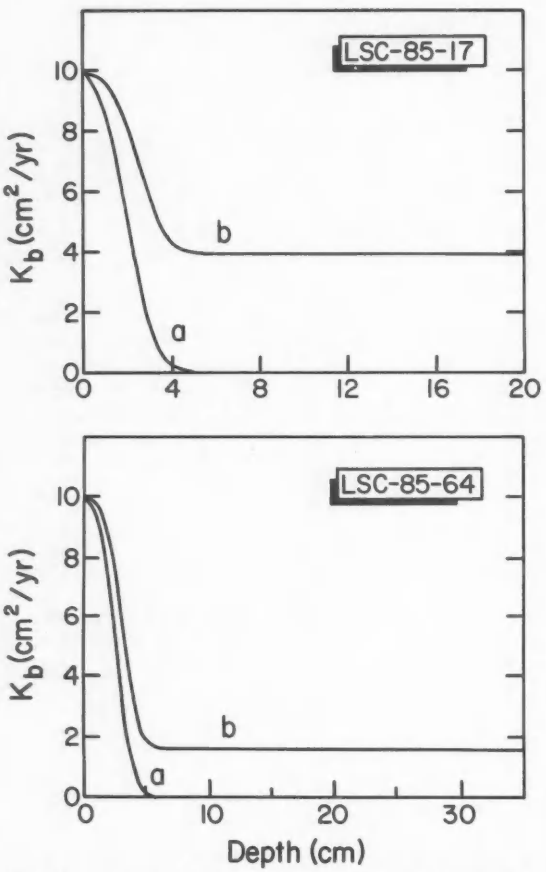

FIG. 6. Depth-dependent diffusive mixing coefficients for the continuous transport and resuspension model (CTR) yielding equivalent ^{210}Pb profiles in core at site 17. (a) Case of advection only ($K_b(\infty)=0$; $w=0.32$ cm·yr^{-1}). (b) Case of mixing only ($K_b(\infty)=3.3$ cm^2·yr^{-1}; $w=0$).

case (a) of the CTR model improves the description of the ^{137}Cs profile (Fig. 7c, dashed line) over the RSSM model. In contrast, the fully diffusive case (b) produces a profile without any peak and considerably overestimates the extent of penetration of ^{137}Cs. In core 64 (Fig. 7d) the clear choice for ^{137}Cs is also (a). This choice preserves the observed structure, although the calculated profile is slightly displaced from the actual peak, while choice (b) fails completely. In all SN cores the advective case (a) consistently describes both excess ^{210}Pb and ^{137}Cs profiles.

The above calculations assume zero resuspension, however. The value of v_r has no effect on the shape of the ^{210}Pb (or any steady-state) distribution. Its effect on the distribution of ^{137}Cs is illustrated for site 17, diffusive case (b), in Fig. 8 where all profiles have been arbitrarily normalized to 1 at $z=0$. As v_r increases from 0 to 3 cm·yr^{-1} a subsurface maximum develops which can approximately reproduce the observed distribution. In general, for pulsed tracer/contaminant inputs, profile peaks can result which are products of the concurrent processes of diffusion and resuspension and are not necessarily faithful records of deposition history. To distinguish, if possible, between these alternative explanations, we solved equation (1) repeatedly as part of an optimization routine in which the resuspension rate varied between 0 and 2 cm·yr^{-1} and w varied between 0 and the maximum value of λ/β. For each choice of w the value of $K_b(\infty)$ was calculated from equation (5). Thus solutions were constrained to those which correctly described ^{210}Pb profiles. Each theoretical profile was least-squares normalized to the observed profile and a standard deviation computed. The resulting standard deviation contour plot for site 17 (Fig. 9) shows the minimum standard deviation (0.22 dpm·g^{-1}) located close to the maximum value of w and minimum value of v_r. In the direction of diminishing advection along the minimum standard deviation path (valley) in this figure (dashed line), similar profiles occur for a roughly linear trade-off between advection and resuspension. The resulting optimized distributions of ^{137}Cs for sites 17 and 64 are shown as in Fig. 7 (c, d solid lines).

The above results are comparable for all the SN cores (Table 3). Transport is primarily advective ($w/w_{max}=78$–94%) but consistently includes small amounts of deep diffusive mixing with values of $K_b(\infty)$ ranging from 0.1–0.5 cm^2·yr^{-1}. In contrast the solution for site 65 indicates no advection. Since the extent of mixing based on ^{210}Pb is small, there is no way within the model framework to transport ^{137}Cs downward sufficiently except through diffusion. Of particular importance is the result that the resuspension rate is negligible in nearly all cases. This result does not imply the absence of resuspension. Rather, in terms of the model, resuspension must occur prior to incorporation of the tracer into the sediment column. Thus the model indicates that sediments capture the net flux of tracer at these sites.

Vertical Distributions of Stable Lead

To confirm that SN cores have primarily recorded a flux history (advection) rather than the effects of mixing we applied the CTR model results to stable lead profiles (for analytical methods see Rossmann 1988). The loading of lead to Lake St. Clair was calculated using the coupled lake model (CLM) with an atmospheric source function constructed by Edgington and Robbins (1976) and extended into the 1980s by Eisenreich et al. (1986). The net flux to sediments was assumed to be proportional to the CLM loading. Model lead profiles were calculated using parameters determined above and normalized to background-subtracted lead distributions. In the comparison of model and measured profiles of total lead (Fig. 10), background concentrations of 12 and 17 ppm Pb for cores 17 and 64, respectively were added to the model profile. In each case the advective solution (a) and the optimized distribution (solid line) are the superior choices, satisfactorily reproducing the data and the peak, in particular, which corresponds to the 1973 atmospheric lead maximum.

Apparent Age of Recent Sediments

If advection is the primary transport process, the apparent age of the recent deposit can be estimated by dividing the thickness of sediment above the textural (by inspection) and compositional (FSOL, Total Carbon) horizon by the model sedimentation rates. This involves an insignificant extrapolation of the dating method since measurable excess ^{210}Pb extends generally to within a few centimetres of this horizon. The mean RSSM model mean age for SN cores is 90 ± 30 yr (Table 4). CTR model ages are slightly higher averaging 110 ± 40 yr. If

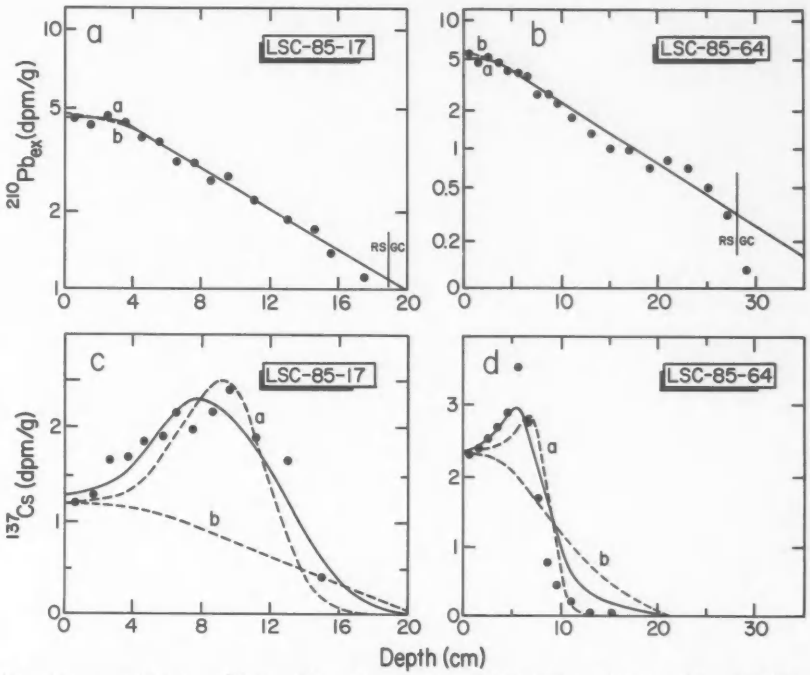

FIG. 7. (top panels) Excess ^{210}Pb profiles and model (a and b) distributions for cores 17 and 64. The vertical line segments locate the break between recent sediments (RS) and glacial clay (GC). (lower panels) Measured and model distributions of ^{137}Cs. Model a consistently describes both tracer distributions. The solid curve is the optimized CTR distribution.

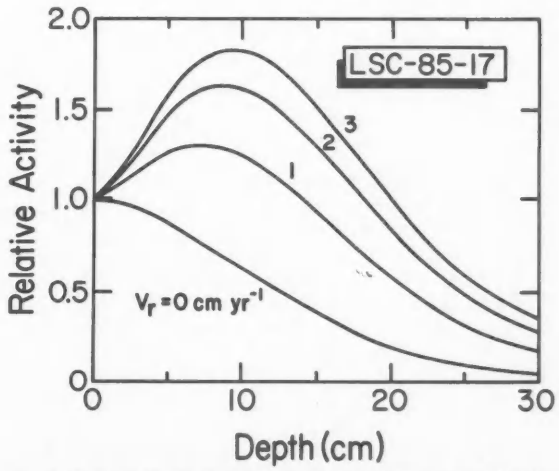

FIG. 8. CTR model distributions based on site 17 parameters for the case of mixing only. Increasing the resuspensions rate, v_r, suppresses surface activities and leads to a subsurface maximum for a tracer pulse. Profiles are arbitrarily normalized to 1 at $z=0$. The curve with $v_r=0$ corresponds to case b.

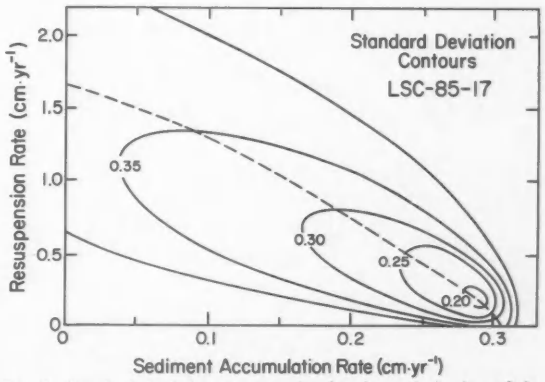

FIG. 9. Standard deviation contour plot for the optimization of the CTR model ^{137}Cs profile (site 17) with respect to v_r and w. The dashed line is the minimum standard deviation path intersecting the global minimum close to $w=w_{max}$ and $v_r=0$.

this latter age applies to the entire deposit (not just to SN cores) then the lake-wide mean accumulation rate is (the mean thickness 7 cm/120 yr) 0.06 cm·yr^{-1} which is roughly 100 times greater than the mean net postglacial accumulation rate. The apparently abrupt onset of net sedimentation in this lake coincides with the period of deforestation and agricultural development of the watershed in the mid 19th century.

Horizontal Distributions and Tracer Storage

The depth of penetration of ^{137}Cs into sediments indicates the net extent of downward transport of a transient tracer pulse occurring about 25 yr earlier. This model-independent quantity should correlate well with the thickness of recent deposits if advection is the primary transport mechanism. The penetration

TABLE 3. Optimized CTR model parameters based on distributions of ^{137}Cs.

Site	β (cm^{-1})	s (cm)	$K_p(\infty)$ ($cm^2 \cdot yr^{-1}$)	v_r ($cm \cdot yr^{-1}$)	w(ctr) ($cm \cdot yr^{-1}$)	w(rssm) ($cm \cdot yr^{-1}$)	w(ctr)/ w(rssm) (%)
17	0.098	2.0	0.32	0.2	0.29	0.32	91
18	0.190	3.0	0.09	0.0	0.15	0.16	94
20	0.257	2.5	0.09	0.0	0.094	0.12	78
21	0.264	3.0	0.05	0.0	0.11	0.12	90
23	0.190	3.0	0.09	0.0	0.15	0.16	94
24	0.121	2.5	0.53	0.0	0.19	0.21	90
64	0.156	2.0	0.13	0.0	0.18	0.20	90
65	0.135	0.2	1.70	0.0	0.00	0.23	0
Means[a]	0.18	2.6	0.18	0.0	0.17	0.18	90
SD	0.06	0.4	0.18	0.1	0.06	0.07	5

[a]Excluding values for site 65.

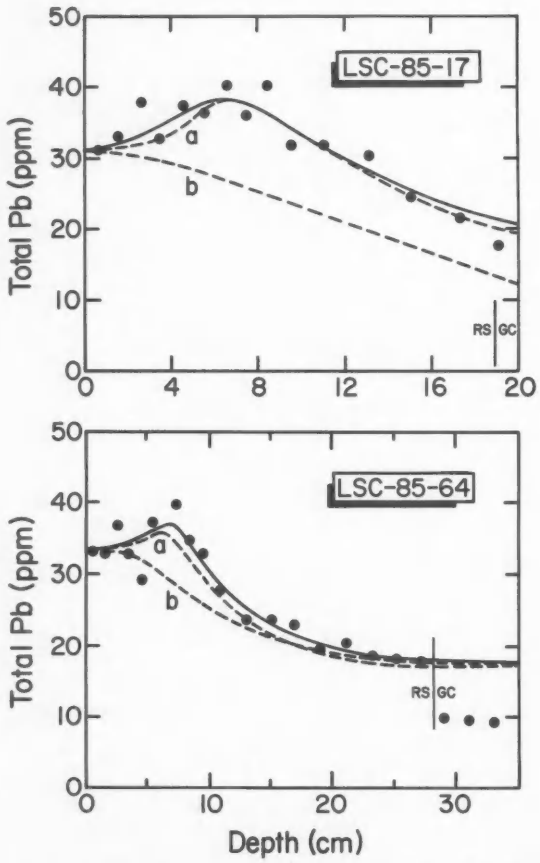

FIG. 10. Measured and model distributions of total lead. CTR model profiles for advective (a) and diffusive (b) cases. The optimized solution is shown as the solid curve.

depth, Z_{pen}, follows the thickness of the recent sediments (H) quite closely ($r=0.85$, $n=33$) with a regression relation: $Z_{pen}(cm) = 2.3 + 0.54\,H(cm)$. This relation indicates that in the absence of a significant deposit thickness ($H=0$) ^{137}Cs still penetrates to an average depth of a few centimetres, presumably because of mixing. There is also a significant relation between

TABLE 4. Apparent age of the glaciolacustrine sediment boundary.

Site	Boundary depth[a] (cm)	RSSM model age (yr b.p.)	CTR model age (yr b.p.)
17	19	60 ± 11	66 ± 12
18	15	80 ± 15	100 ± 19
20	13	76 ± 20	130 ± 35
21	17	120 ± 18	150 ± 23
23	17	94 ± 30	110 ± 36
24	15	65 ± 10	80 ± 12
64	28	140 ± 10	160 ± 11
65	17	52 ± 10	∞[b]
Means[c]	18	90 ± 30	110 ± 40

[a]Uncertainty in boundary location: ±2 cm.
[b]Overall uncertainty in age assignments includes errors in (1) the least-squares determined slope of log excess ^{210}Pb, (2) the estimate of unsupported ^{210}Pb, and (3) the boundary location.
[c]Means exclude site 65 values.

the thickness of recent sediments and the surface (0–1 cm) activity of ^{137}Cs (Fig. 11a, $r=0.66$, $n=33$) and particularly the total accumulation (vertically integrated) ^{137}Cs (Fig. 11b, $r=0.82$, $n=33$). The central area in Fig. 11b (>30 $dpm \cdot g^{-1}$) corresponds to sites 38 and 69 which possess anomalously high amounts of ^{137}Cs, 58 and 117 $dpm \cdot cm^{-2}$, respectively. From contour integration, the total accumulation of ^{137}Cs in sediments as of 1985 is estimated as 1369 GBq corresponding to an average of 7.4 $dpm \cdot cm^{-2}$. Since the total decay-corrected loading was 17.39 TBq, roughly 8% of all the ^{137}Cs which entered the lake was retained as of 1985. The mean excess ^{210}Pb storage in the lake can be estimated from the mean ratio of ^{137}Cs to excess ^{210}Pb storage in SN cores: 0.51. Excess ^{210}Pb storage is then $7.4 / 0.51 = 14.5$ $dpm \cdot cm^{-2}$. If all ^{210}Pb entering the lake were retained, the mean storage (standing crop) would be the loading ($dpm \cdot cm^{-2}$) / decay constant (λ) = $3.5 / 0.03114$ = 112 $dpm \cdot cm^{-2}$. Thus about 13% of the steady-state inventory of excess ^{210}Pb is retained in sediments.

The mean activity of ^{137}Cs in surface (0–2 cm) sediments in 1976 (Fig. 12a) was considerably higher than in 1985. To compare these results with 1985 data we reconstructed the activity in the 0- to 2-cm interval at each site from measured ^{137}Cs profiles. Distributions of ^{137}Cs were vertically integrated (by summing the product of activity per gram and mass per square centimetre of each interval) from 0 to 2 cm (Fig. 12b). The resultant inventory was divided by the cumulative sediment weight to obtain the reconstructed value. We simulated the possible effect of losses of surface material in grab sampling by

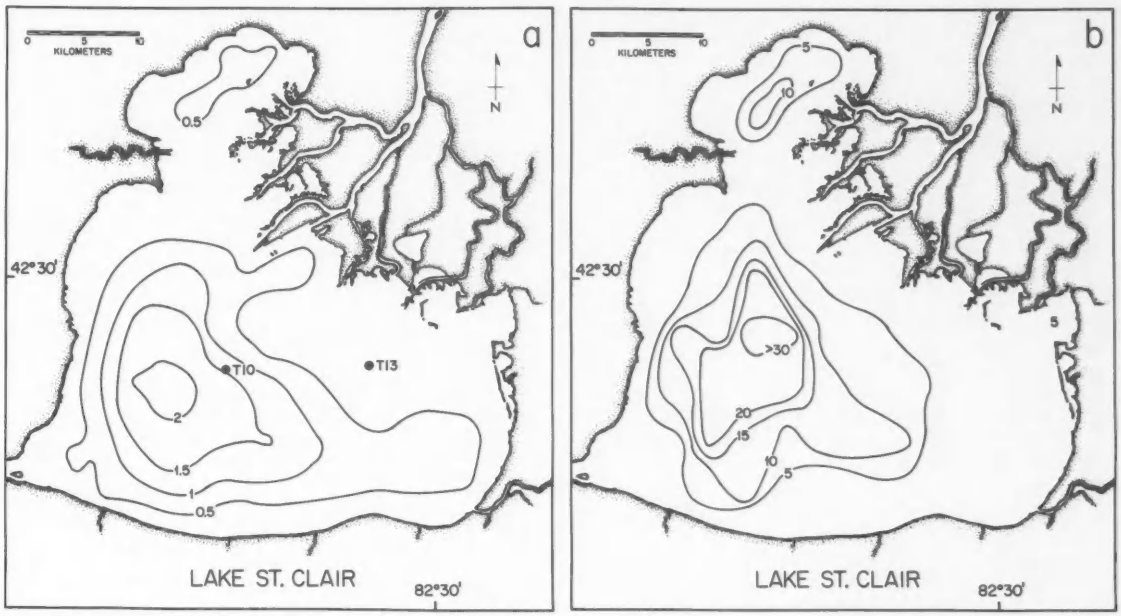

FIG. 11. (a) Activity of ^{137}Cs in surface sediments (0–1 cm) and trap site locations. (b) Total ^{137}Cs accumulation (dpm·cm^{-2}). Anomalously high accumulation (shaded region with >30 dpm·cm^{-2}) occurs in cores with marked stratigraphic inhomogenieties.

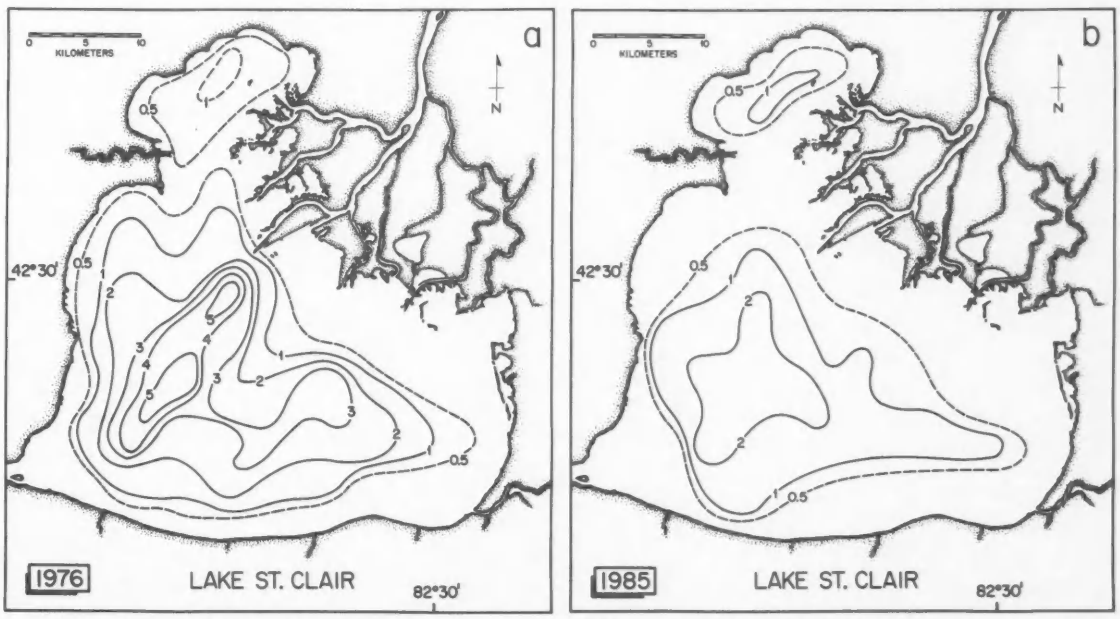

FIG. 12. (a) Activity of ^{137}Cs in surface sediments (0–2 cm) collected by Shipex grab sampling in 1976. (b) Activity in the 0–2 cm interval calculated from profiles in cores collected in 1985. Only 20% of the decrease resulted from radioactive decay.

repeating the calculation assuming 1 and 2 cm of sediment was scoured away on sampling. Such losses had a small effect on the estimate of accumulation (20% or less) because the higher water content of surface materials reduces the amount which those levels contribute to the total. ^{137}Cs activities are as much as 2.5 times higher at some sites in 1976 than in 1985 but only 19% of the difference is ascribable to radioactive decay.

Since little additional ^{137}Cs entered the lake during this 9-yr period, the ratio of 1985 surface ^{137}Cs to 1976 values (decay-corrected to 1985) is a measure of the removal of the isotope

from the surface. Over limited areas of the lake bottom there was more than a 50% reduction in activity while elsewhere within the main body of the deposits it was between 25 and 50%. The smallest reductions occurred toward the margins where higher proportions of coarse material (sand) may have occluded fine-grained sediments containing ^{137}Cs and hindered its removal.

Mean Particle Residence Times

The depositional basins of the main lakes serve as permanent, closed-system, burial sites for particle-associated contaminants, although horizontal redistribution of tracers such as ^{137}Cs can continue to take place over decades (Edgington and Robbins 1989). In contrast, recent deposits in Lake St. Clair are not a closed system since resuspension presumably results in transfer of material out of the lake. According to Thomas et al. (1977) the reduction in surface activities of mercury and certain persistent chlorinated organic compounds in the early 1970s was due mainly to this process. However surface concentrations could have also declined through downward transport. To distinguish between these removal mechanisms, one should determine changes in storage over time since this quantity is sensitive to net exportation but not to downward transfer.

While changes in ^{137}Cs storage are not available, its residence time in sediments may be inferred by comparison of storage, concentrations, and loadings. We employ a two-layer model with a resuspension term to represent the horizontally averaged characteristics of the deposit. The flux of tracer entering the lake, F (dpm·cm^{-2}·yr^{-1}) is incorporated into a resuspendable sediment pool (I) of mass per unit area, G (g·cm^{-2}). We use mass units here to keep the transport equations in simple form. Note that the RSSM model mixed layer may not correspond to this pool because of the effects of horizontal sediment redistribution as well as averaging. The total storage in the pool I is given by:

$$(8)\quad dS_I/dt = F - (\lambda + \lambda_I)S_I$$

where λ is the radioactive decay constant and λ_I is the removal rate constant characterizing the combined rates of loss from the mixed layer through resuspension and burial.

$$(9)\quad \lambda_I = (R_o + R_n)/G$$

where R_o is the mean net resuspension rate (g·cm^{-2}·yr^{-1}). This quantity is the rate at which mass is exported from the system through resuspension. It is not the mass flux as measured by sediment traps. R_n is the mean net sediment accumulation rate and the total mass flux is $R = R_o + R_n$. The amount stored in region II below the mixed layer is given by:

$$(10)\quad dS_{II}/dt = \lambda_{II} S_I - \lambda S_{II}$$

where $\lambda_{II} = R_o/G$. The total stored in the deposit is then $S_I + S_{II}$ while the total amount which would be present in a closed system (without resuspension losses), S_T, is given by:

$$(11)\quad dS_T/dt = F - \lambda S_T.$$

The fraction of tracer retained in the deposit is defined as:

$$(12)\quad Fr = (S_I + S_{II})/S_T.$$

The mean activity of tracer in the mixed layer then,

$$(13)\quad A = S_I/G.$$

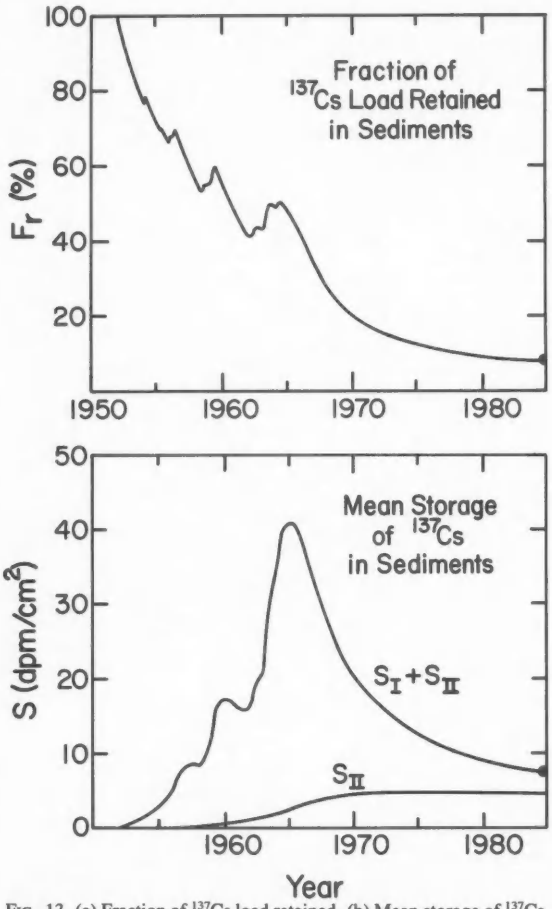

FIG. 13. (a) Fraction of ^{137}Cs load retained. (b) Mean storage of ^{137}Cs. Model results with a resuspendable pool mass of 4.5 g·cm^{-2} and residence time (T_I) of 3 yr.

For ^{137}Cs the model is evaluated using the loading function (Fig. 2) for F and a value of R_n obtained above of 0.08 g·cm^{-2}·yr^{-1} (0.06 cm·yr^{-1}). The values of G and λ_I which reproduce the observed value of Fr and A in 1985 are 4.5 g·cm^{-2} and 0.33·yr^{-1}, respectively. The residence time of the tracer in the mixed layer is $\lambda_I^{-1} = 3$ yr. The value of λ_{II} is 0.08/4.5 = 0.02·yr^{-1}. The net resuspension rate constant is then $\lambda_I - \lambda_{II} = 0.31 \cdot yr^{-1}$ which imlies a net mass exportation rate of $0.31 \times 4.5 = 1.4 g \cdot cm^{-2} \cdot yr^{-1}$. The ratio of rate constants for net resuspension and sedimentation $(\lambda_I - \lambda_{II})/\lambda_{II} = 16$) indicates the relative importance of these processes. Resuspension appears to be 20 times more efficient than sedimentation in diminishing surface tracer concentrations. The fraction retained (Fig. 13 top panel) and storage (Fig. 13 bottom panel) versus time are calculated as solutions to the above differential equations. By definition the curves intersect the data points. However the mean surface activity in 1976 is an independent quantity which is correctly predicted by the model (Fig. 14).

For excess ^{210}Pb, steady-state conditions ($dS_I/dt = dS_{II}/dt = dS_T/dt = 0$) result in simplified relations from which it can be shown that the fraction retained is given by:

$$(14)\quad Fr = (\lambda + \lambda_{II})/(\lambda + \lambda_I)$$

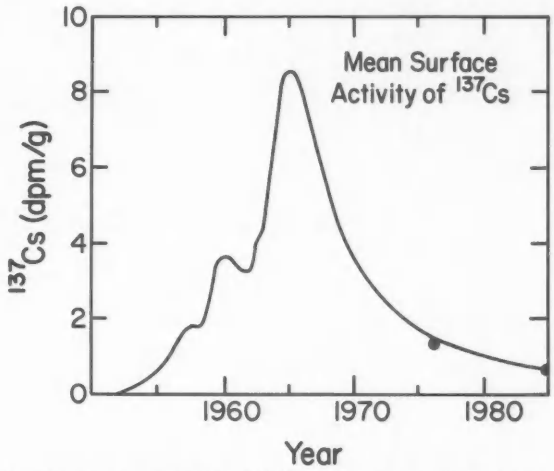

FIG. 14. Model mean activity of ^{137}Cs in the resuspendable pool. The mean value in 1976 is correctly predicted by the model.

TABLE 5. Mean residence times of tracers and contaminants in surface sediments of Lake St. Clair.

Constituent	Residence time (yr)	Reference
Cesium-137	3.0[a]	This study
Excess lead-210	3.0[a]	This study
Mercury	4.0	Thomas et al. (1975)
DDE	3.6	Frank et al. (1977)
TDE	4.6	Frank et al. (1977)
DDT	2.9	Frank et al. (1977)
Total PCBs	6.2	Frank et al. (1977)
Mean	4 ± 1	

[a]Surface mixed layer residence time based on the two-layer model.

with $\lambda = 0.03114 \cdot yr^{-1}$ for ^{210}Pb. Using the ^{137}Cs derived values for λ_I and λ_{II} we calculate $Fr = 14\%$ as compared with a measured value of 13%. Thus within experimental errors the two layer model accounts satisfactorily for the average transport characteristics of both tracers in the deposit.

The model is consistent as well with the mean residence times inferred for other more poorly characterized constituents. From the above equations it follows that if the flux to the deposit ceases at some point ($F = 0$ in equation (1)), the surface sediment concentrations of contaminant will decrease at subsequent times according to the relation

$$(15) \quad C = C_o \exp(-\delta t\,(\lambda + \lambda_I))$$

where λ is either the decay constant in the case of radioactive elements or the first-order degradation rate constant in the case of compounds subject to in situ chemical change. The tracer/contaminant residence time in the surface layer is then

$$(16) \quad T_I = 1 / (-\lambda + \ln(C_o/C)\delta t)$$

where δt is the time between mean concentration measurements C_o and C. This relation may be used to estimate residence times associated with changes in mean surface concentrations of mercury (Thomas et al. 1977) and chlorinated organic compounds (Frank et al. 1977) between 1970 and 1974. The calculation is necessarily approximate since it must be assumed that loads to the lake between 1970 and 1974 were negligible in comparison

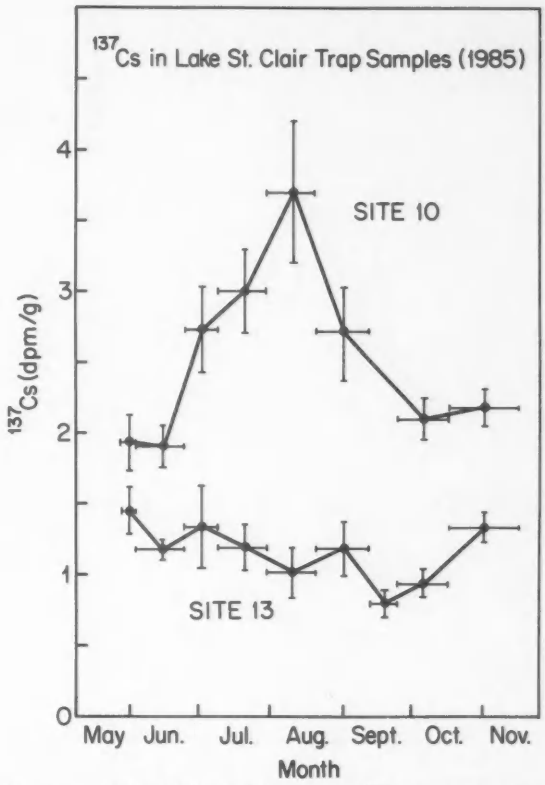

FIG. 15. Seasonal variation in the activity of ^{137}Cs in trap materials collected at two sites in Lake St. Clair. Site T10 receives more inflow of ^{137}Cs-active particles than T13, especially during the summer months.

with those in the 1960s and that the organics were not subject to degradation ($\lambda = 0$). The results (Table 5) show that residence times are compatible averaging about 4 ± 1 yr. The largest discrepancy is for PCBs where continued inputs between 1970 and 1974 may have increased the apparent residence time.

^{137}Cs in Sediment Traps

The activity of ^{137}Cs in trap samples (Fig. 15) contrasts markedly between stations. At station T-10 (Fig. 1a) it is about 2 $dpm \cdot g^{-1}$ during May and June and rises to a maximum of 3.7 $dpm \cdot g^{-1}$ by the end of July, decreasing thereafter to about 2 $dpm \cdot g^{-1}$ by October. At site T-13 the activity declines steadily from 1.45 $dpm \cdot g^{-1}$ in early June to 0.8 $dpm \cdot g^{-1}$ by mid-September, thereafter rising toward the previous early June value. The activity of ^{40}K (Table 6) shows no significant change with time at either site.

Particles collected by traps have three major sources: authigenic production, inflow, and resuspension. The constancy of the ^{40}K data suggest that the former source does not contribute significantly to the mass of trap material. Particles entering traps from inflow of Lake Huron water have a ^{137}Cs activity of about 20 $dpm \cdot g^{-1}$ in 1985 based on a total activity in water of 0.06 $dpm \cdot L^{-1}$ (Robbins 1985b), a partition coefficient of 3×10^5 $mL \cdot g^{-1}$ (Alberts and Whalgren 1981) and a mean suspended matter activity of 0.5 ppm. The ^{137}Cs activity in surface sedi-

TABLE 6. ^{137}Cs and ^{40}K in trap samples collected at sites T10 and T13 in Lake St. Clair (1985).

Location-sample number	Collection period	Cesium-137 ($dpm \cdot g^{-1}$)[a]	Potassium-40 ($dpm \cdot g^{-1}$)[a]
T10 -401	5/30–6/5	1.93 ± 0.20	30 ± 4
-402	6/5–6/26	1.90 ± 0.15	34 ± 3
-403	6/26–7/10	2.73 ± 0.30	34 ± 10
-404	7/10–7/31	3.00 ± 0.30	22 ± 8
-405	7/31–8/21	3.70 ± 0.50	26 ± 10
-406B	9/13–9/25	2.71 ± 0.34	37 ± 10
-408	9/25–10/17	2.10 ± 0.15	27 ± 3
-410	10/17–11/17	2.19 ± 0.13	37 ± 3
Mean		2.5 ± 0.6	30 ± 6
T13 -401	5/30–6/5	1.45 ± 0.17	34 ± 4
-402	6/5–6/26	1.17 ± 0.06	33 ± 2
-403	6/26–7/10	1.33 ± 0.30	30 ± 9
-404	7/10–7/31	1.19 ± 0.16	33 ± 4
-405	7/31–8/21	1.01 ± 0.18	33 ± 6
-406	8/21–9/13	1.18 ± 0.19	33 ± 5
-406B	9/13–9/25	0.80 ± 0.10	32 ± 3
-408	9/25–10/17	0.94 ± 0.10	30 ± 2
-410	10/17–11/17	1.33 ± 0.11	35 ± 3
Mean		1.2 ± 0.2	30 ± 2

[a]Reported uncertainties are analytical errors.

ments of Huron (Robbins et al. 1977 and Robbins 1980) is also around 20 $dpm \cdot g^{-1}$. In contrast, the ^{137}Cs activity of resuspended sediment presumably reflects surface activities which are about 2 $dpm \cdot g^{-1}$ or less (Fig. 11a). Thus the activity of ^{137}Cs on inflowing particles probably exceeds activities on resuspended surface sediments by at least an order of magnitude.

This contrast can be used to infer the origins of trap material. During the summer months when the lake is less mixed physically, resuspension contributes less to trap material and the horizontal mixing of inflow particles should be less efficient. Charlton and Oliver (1986) observed low resuspension rates during the period from July through September. During this period a trap at site T-10 located along the direct course of water flow between the St. Clair and Detroit River should have collected a higher proportion of inflow particles. The more remote trap at site T13, in shallower water, should have received a greater proportion of resuspended material. Site T10 is situated over sediments where the surface activity (0–1 cm) is about 1.5 $dpm \cdot g^{-1}$ (Fig. 11a). In early June and again after mid-September, levels in traps at this site closely match surface sediment activities. In contrast site T-13 is situated over sediments with an activity of 0.2 $dpm \cdot g^{-1}$. During the early period, the activity is close to that at site T-10 but as the season progresses values decrease, presumably because reduced horizontal mixing results in higher proportions of locally resuspended material. However the activity does not decrease to the value in sediments directly under the trap presumably because (1) inflow particles still contribute, (2) horizontal water motions bring resuspended materials of higher activity to the site, and (3) fine particles of higher specific ^{137}Cs content may be preferentially resuspended especially over marginal deposits.

The net resuspension flux estimated above as 1.4 $g \cdot cm^{-2} \cdot yr^{-1}$ is considerably less than the average gross downward flux as measured by traps. The seasonally-weighted mean trap flux (all sites) based on the study by Charlton and Oliver (1986) is about 200 $g \cdot m^{-2} \cdot d^{-1}$ or about 7 $g \cdot cm^{-2} \cdot yr^{-1}$. Thus only a fraction (20%) of the average trap flux is exported annually from the lake. The remainder is presumably reincorporated into the resuspendable sediment pool. The reciprocal of this fraction, 1./0.2 = 5 yr, is an independent measure of residence time which is consistent with the two-layer model residence time of particles in this pool.

Conclusions

Although Lake St. Clair has been considered a nondepositional environment in terms of net postglacial accumulation, significant activities of fallout ^{137}Cs and excess ^{210}Pb were found in fine-grained sediments over a wide area and have penetrated to considerable depths in recent deposits. Despite the rapid flushing of the lake, sediments retained 8% of the ^{137}Cs as of 1985 and 13% of the potential standing crop of excess ^{210}Pb. Profiles of radiotracers and bulk sediment characteristics revealed stratigraphic inhomogenieties in cores located in the vicinity of the shipping channel and "stratigraphically normal" (SN) cores clustered in the southern and deepest part of the lake. In SN cores, tracer distributions were described consistently by vertical transport models indicating intense mixing of near-surface sediments over a range of several centimetres and primarily advection below. A single set of model values for mixing and sedimentation rates consistently described ^{137}Cs, ^{210}Pb as well as contaminant Pb profiles. Models indicate that at these sites resuspension takes place prior to incorporation of tracers into permanent deposits. In SN cores an approximate history of lake contamination (for particle-associated contaminants) may be retrieved from the sedimentary records. Recent sediments appear to have begun forming about 110 yr ago in coincidence with wide-spread agricultural development of the region. The horizontally-averaged characteristics of the deposit indicate a resuspendable pool mass of 4.5 $g \cdot cm^{-2}$ and a residence time of 3 yr. This time is consistent with model calculations for the residence times of Hg, PCBs, and DDT plus its degradation products in surface sediments. Trap-collected materials from two mid-depth sites show markedly contrasting seasonal variations in ^{137}Cs activity which reflect the site and time-dependent proportions of settling particles from the two principal particle sources: resuspension and inflow. The high specific activity of ^{137}Cs on inflow particles as compared with resuspended sediments may be used to trace particulate matter circulation in this lake. Only a fraction (ca. 20%) of material resuspended is lost from the system annually.

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Storage and Dynamics of Subsurface Detritus in a Sand-Bottomed Stream

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Metzler, G. M., and L. A. Smock. 1990. Storage and dynamics of subsurface detritus in a sand-bottomed stream. Can. J. Fish. Aquat. Sci. 47: 588–594.

Annual mean storage of buried detritus (0–20 cm depth) in a first-order, sand-bottomed stream was 4.8 kg AFDM/m^2, approximately one order of magnitude greater than surface storage. Forty percent of the buried detritus was wood >8 mm; much of the remainder was 1–8 mm particles. Exchange of detritus between surface and shallow sediments occurred throughout the year; exchange between surface and deep sediments occurred only during spates. Heavy rainfall during a September hurricane caused a mean scour depth of 6 cm (range = 0–27 cm) and contributed to a 0.94 kg/m^2 reduction of buried detritus. Buried leaves were processed slower than leaves on the sediment surface (25% of initial buried leaves remained after 1 yr). Particles <8 mm were processed faster from January to March (19% mass reduction) than at other times (8–9% mass reduction). Except during the September spate, burial was approximately offset by decomposition. About 21% of estimated autumnal leaf input to the stream became buried. Given the large quantity of detritus stored in the subsurface, its slow processing rate and the episodic nature of its release from deep storage, the hyporheic area of this stream has an important effect on the stream's carbon spiralling length, energetics, and trophic dynamics.

Le stockage moyen annuel de détritus enfouis (0–20 cm de profondeur) dans un cours d'eau à fond sableux de premier ordre s'élevait à 4.8 kg AFDM/m^2, soit environ un ordre de grandeur de plus que le stockage en surface. Quarante pour cent des détritus enfouis étaient constitués de débris ligneux de moins de 8 mm; le restant était composé en grande partie de particules de 1–8 mm. Les échanges de détritus entre la surface et les sédiments peu profonds se font pendant toute l'année; des échanges entre les sédiments de surface et les sédiments en profondeur ne se font que pendant la crue nivale. Les fortes précipitations qui ont eu lieu pendant un ouragan en septembre ont entraîné un décapage sur une profondeur moyenne de 6 cm (fourchette de 0–27 cm) et ont contribué à une réduction de 0.94 kg/m^2 de détritus enfouis. Les feuilles enfouies se décomposaient plus lentement que les feuilles situées à la surface des sédiments (25 % des feuilles enfouies au début n'étaient pas encore décomposés après un an). Les particules de granulométrie inférieures à 8 mm se décomposaient plus rapidement entre janvier et mars (19 % de réduction de masse) qu'à d'autres époques de l'années (8–9 % de réduction de masse). Sauf pendant la crue nivale de septembre, l'enfouissement était à peu près compensé par la décomposition. Environ 21 % de l'apport estimatif en feuilles dans le cours d'eau en automne sont enfouis. Compte tenu de la grande quantité de détritus stockés sous la surface, de la lenteur de leur taux de décomposition et de la nature épisodique de leur libération lorsqu'ils sont enfouis, la zone hyporhéique de ce cours d'eau a un effet important sur la longueur de la spirale du carbone du cours d'eau, sur ses caractéristiques énergétiques et sa dynamique trophique.

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Studies on organic matter dynamics in streams have focused mainly on the sediment surface and water column, conceptually and operationally viewing streams as one-compartment systems. Some recent studies, however, have viewed riparian areas, especially floodplains, as a system compartment rather than simply as a source of organic matter, thus providing a more comprehensive and integrated view of organic matter dynamics in streams (Mitsch 1979; Minshall et al. 1985; Cuffney 1988). The general importance of a third compartment, the hyporheic zone or area within the sediment but above groundwater, has been noted (Danielopol 1980; Hynes 1983; Williams 1984), but specifics of the importance of this area to stream functioning have been neglected.

Most hyporheic zone research by ecologists has focused on invertebrates, a wide variety of often abundant species being found deep in the sediment (Williams 1984). The importance of the hyporheic zone to stream metabolism was noted by Grimm and Fisher (1984). This area also can be important to organic matter dynamics. Some studies suggest that storage in the hyporheic zone may be considerably higher than on the surface (Herbst 1979; Cummins et al. 1983), partly because buried detritus has a slower decomposition rate (Herbst 1980; Rounick and Winterbourn 1983) and a lower probability of downstream transport during spates. However, the dynamics of organic matter inputs, decomposition during storage, and export to the surface are relatively unknown.

Sediment particle size is an important factor controlling hyporheic zone processes and the degree of coupling of the channel surface and subsurface. Rates of chemical and material exchanges decrease as particles become smaller (Beschta and Jackson 1979; Moring 1982), for example decreasing move-

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ment of organic matter and dissolved oxygen. Sediment stability, which is a function of particle size, is an important determinant of organic matter retention time within sediment, especially during spates. While larger particles are relatively stable, sand has a low erosion velocity and thus is very unstable (Ingle Smith and Stopp 1978). The depth of scour during spates in sandy streams can be deep compared with streams with other types of sediment; hence the probability of organic matter being buried and/or released in sandy streams is high. Because of the potentially higher frequency of hyporheic zone disturbance and the lower amounts of detritus storage on the surface of sand-bottomed streams versus streams with larger substrates (L. A. Smock, unpubl. data), consideration of hyporheic zone processes as well as the coupling of subsurface and surface areas may be critical for an understanding of organic matter dynamics in sandy streams.

We examined particulate organic matter dynamics in the hyporheic zone of a southeastern United States sand-bottomed, headwater stream, focusing on seasonal changes in detritus storage and processing rates of various sizes of coarse particulate organic matter (CPOM; >1 mm) and fine particulate organic matter (FPOM; 1 mm to 0.45 μm). The magnitude of sediment scour and deposition also was determined, and this information was used in conjunction with the storage and processing data to estimate amounts of detritus transported into and released from the hyporheic zone of the stream.

Study Site and Methods

The study was conducted in Buzzards Branch, a first-order, blackwater stream in Surrey County, Virginia on the Coastal Plain of the southeastern United States. The stream had a low gradient (0.08%), mean bankfull width of 2.5 m and mean depth of 25 cm. Mean annual discharge in 1984 was 0.08 m^3/s (range = 0.006–0.269 m^3/s; L. A. Smock, unpubl. data), but was not monitored during this study. Annual mean water temperature during 1984–85 was 16°C and annual mean pH was 5.7 (Harlowe 1985). The stream meandered through a nearly fully-canopied floodplain dominated by black gum (*Nyssa sylvatica* var. *biflora*, water ash (*Fraxinus caroliniana*), and red maple (*Acer rubrum*).

The substrate was a uniform loose medium-fine sand (median phi = 2.1) with some silt along the banks. The sand typically extended downward 15–40 cm to clay. Interstitial flow rates, measured with dye injections, were very slow, ranging from nondetectable to 1.4 cm/h (Metzler 1987). Whereas dissolved oxygen concentrations in surface waters always were close to saturation, near anaerobic conditions occurred 5 cm below the sediment surface during the summer and early autumn and below 10 cm during the remainder of the year (Metzler 1987; Strommer and Smock 1989).

Bankfull discharge (0.25 m^3/s) was exceeded three times during the study, twice during August and once in September 1985. Highest discharge was associated with a September spate that resulted from Hurricane Gloria, when 16.5 cm of rain fell in 1 d. Water depth reached 42 cm above bankful, with complete inundation of the floodplain. Sand deposited on the floodplain indicated that sediment had been transported from the channel during the spate.

Detritus storage

Detritus storage within the sediment was measured in a 40-m section of stream. Preliminary sampling showed that this section could be divided into areas with either relatively high or low organic content, the former near banks and upstream of debris dams and the latter in midstream. The stream section was mapped to delineate these two areas (designated high (HOC) and low organic content (LOC)), and the proportional distribution of these areas determined. This separation provided the basis for a stratified random sampling scheme that reduced sample variance.

Sixteen sediment samples were collected from both the HOC and LOC areas four times from July 1985 to May 1986 using a 5.2-cm inner-diameter corer. Detritus lying on the sediment surface was brushed away, the corer was driven about 30 cm into the sediment, and after extraction the top 20 cm was separated into four size fractions (0.053–0.15 mm, 0.15–1 mm, 1–8 mm, >8 mm) by wet sieving. The >8-mm fraction then was visually separated into woody and nonwoody fractions. Ash free dry mass (AFDM) in each fraction was calculated after drying (48 h at 60°C) and ashing (4 h at 550°C). Detritus storage in the stream was calculated by adding the HOC and LOC concentrations weighted by the fraction of streambed each area covered (HOC = 25%; LOC = 75%). For the May sampling, 20 of the 32 cores also were separated into 0–10 cm and 10–20 cm sections to examine the vertical distribution of buried detritus.

Sediment dynamics

Sediment scour and deposition were monitored using columns of coloured sand implanted into the sediment (Metzler 1987; also see Strommer and Smock 1989). A pipe (3 cm diameter × 30 cm long) fitted with a point was driven into the sediment. Coloured sand was poured into the pipe. The pipe was then slowly pulled upward while tamping down the coloured sand, thereby leaving the column in the sediment. Columns were embedded in the center of HOC and LOC areas at two to three locations across the stream every 2 m over the 40-m section of stream used for the storage study. Distance of the top of a column, which was initially even with the sediment surface, to a constant overhead reference point was measured six times over 16 mo, including times when detritus storage was determined. Maximum depth of scour was determined as the change in distance from the reference point to the top of the coloured sand column. The height of uncoloured sediment lying over the coloured sand column measured net deposition of sediment. After measurements were made, columns were brought up to the level of the sediment surface with additional coloured sand.

Detritus processing

Processing rates of whole leaves were determined with standard litter bag techniques. About 5 g of unleached, air-dried leaves of either black gum, water ash, or red maple, collected in the fall of 1984 from the floodplain of Buzzards Branch, were placed in nylon mesh bags (2 mm pore size). Initial AFDM in each bag was calculated using a conversion factor relating AFDM to air-dry mass. On 3 December 1984, five bags of each species were tied to stakes and buried about 10–20 cm below the surface over a 200-m stretch of stream. All bags on one stake were recovered approximately monthly over 15 mo. Contents of leaf bags were oven-dried (48 h at 60°C) and ashed (4 h at 550°C) to determine remaining AFDM. Exponential processing rates were calculated by regressing ln(percent AFDM remaining) against time. Analysis of covariance (ANCOVA)

was used to test for differences in processing rates of the three species.

Net processing rates of smaller sizes of detritus were determined in buried cores. Sediment and associated detritus were collected from the stream's hyporheic zone approximately 2 wk before the start of an experiment. Material retained by an 8-mm mesh sieve was discarded to remove large wood and then 1.5–2 g of leaf fragments >8 mm were added to the <8 mm fraction. After air-drying, sediment was placed into 30 × 5 cm plastic cores sealed at the bottom and with numerous 1-cm holes drilled in the sides.

Five cores were randomly selected for immediate sieving of material into four size fractions; mean AFDM of each fraction in these cores estimated initial AFDM in the remaining cores. Five other cores then were embedded into sediment in both the HOC and LOC areas. This was repeated three times over 1 yr. Cores were recovered after 72–78 d, coinciding with storage measurements, and AFDM in each size fraction was determined. Net processing of each size fraction was calculated as percent reduction of AFDM.

Detritus burial and release

Net transport of detritus into or out of the sediment (i.e. burial or release) was estimated for three time periods using storage and processing data. Transport was calculated as

$$(1) \quad -T = R_p A - B$$

where T is the net mass of detritus transported into or out of the sediment over a time period, A and B are the mass of detritus stored in the sediment at the beginning and end of the time period, respectively, and R_p is the rate of detritus processing expressed as a fractional reduction over the time period. The negative sign is used so that transport from storage (= release) is a negative number and transport into the sediment (= burial) is a positive number. To test whether transport was significantly different from zero over a time period, two-sided t-tests were run with infinite degrees of freedom. Variance (S^2) associated with T was estimated as

$$(2) \quad S^2 = A^2 S_{Rp}^2 + (E(R_p))^2 S_A^2 + S_A^2 S_{Rp}^2 + S_B^2$$

where E is the expected value (Mood et al. 1974).

Results

Detritus storage

Detritus storage (>0.053 mm; 0–20 cm depth) ranged from 5.8–6.7 kg/m^2 in the HOC area to only 3.9–4.8 kg/m^2 in the LOC area. The vertical distribution of detritus was homogeneous in the top 20 cm of sediment, based on comparison of AFDM of each size class in the 0–10 cm and 10–20 cm sections of cores collected in May (t-test; $P>0.05$). Annual mean storage, calculated by weighting storage in each area by the proportional abundance of that area, was 4.8 kg/m^2. Annual mean storage of detritus exclusive of wood >8 mm was 2.9 kg/m^2. Total detritus storage over the year fluctuated <8% of the mean (Fig. 1). When large wood was excluded, however, 30% more detritus was present at the beginning of August than at any other time (ANOVA and Duncan's Multiple Range Test, $P<0.05$).

Large wood and particles 1–8 mm were the most abundant sizes (Fig. 1). Their abundance did not vary significantly ($P>0.05$) during the study. Little nonwoody material >8 mm was found buried over the year. There were no significant ($P>0.05$) differences in storage of any size classes of detritus from October through May, but a significant decrease of about 40% of late July storage of particles <1 mm did occur between August and October (ANOVA and Duncan's Multiple Range Test; $P<0.05$). This coincided with the period of high discharge associated with the hurricane. Two factors probably were responsible for the difference in the amount of change in storage of larger versus smaller particles. Reburial of larger, heavier particles was faster than for smaller particles. Also, large particles constituted the majority of detritus on the sediment surface and floodplain during August through October (L. A. Smock, unpubl. data). Burial of a portion of this material no doubt occurred as the storm flow receded.

Sediment dynamics

Sediment movement in Buzzards Branch was highly heterogeneous both spatially and temporally (Table 1; Fig. 2). Great-

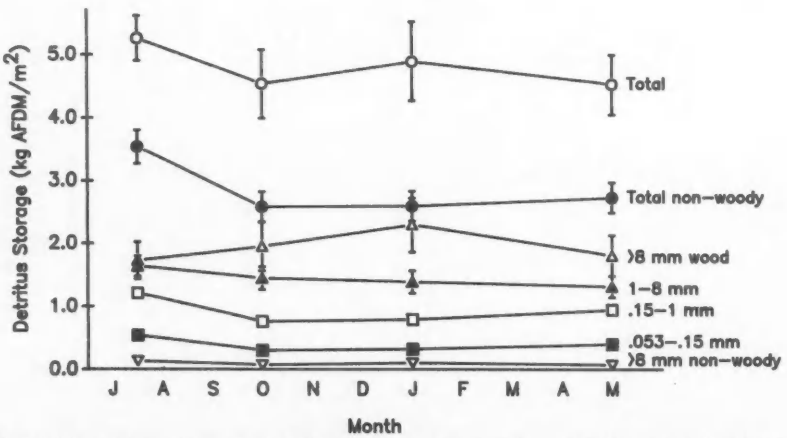

FIG. 1. Mean detritus storage (as AFDM with ±1 SE) in the top 20 cm of sediment, calculated as the weighted mean of storage in HOC and LOC areas.

TABLE 1. Depth of sediment scour and net change in sediment level in areas of high (HOC) and low organic content (LOC). Combined values were calculated by adding values from the HOC and LOC areas weighted by the proportional abundance of each area in the stream.

Time period (1985–86)	Depth of scour (cm)			Net change in level (cm)		
	HOC	LOC	Combined	HOC	LOC	Combined
Apr. 19–July 11	1.7	2.5	2.3	+0.5	−0.2	0
July 11–Oct. 6	7.3	5.5	6.0	−1.2	+3.8	+2.6
Oct. 6–Jan. 16	3.3	0.9	1.5	+2.2	−0.2	+0.4
Jan. 16–May 11	2.6	4.2	3.8	+1.2	−1.0	−0.4
May 11–Aug. 11	2.7	4.7	4.2	−0.9	−1.5	−1.3

est mean scour (6 cm, weighted mean) occurred between July and October, associated with the heavy rainfall. Least scour (1.5 cm) occurred from October to January. During this time, mean scour in the LOC area was only 0.9 cm, much lower than during any other time period. Mean net change in sediment level over the study was small (Table 1). The greatest change occurred from July to October when there was a net loss of 1.2 cm in the HOC area and a net gain of 3.8 cm in the LOC area for an overall 2.6 cm deposition.

Spatial differences in amounts of scour and sediment deposition caused considerable change in sediment longitudinal profiles. This was particularly true of deposition associated with the September hurricane (Fig. 2). Aggradation that occurred during this time was followed by a long period of degradation. Nearly 1 yr after the storm, however, mean sediment level in the stream was still 1.3 cm higher than prior to the storm.

The longitudinal profiles (Fig. 2) also show that, during July–October, both net deposition and loss of sediment occurred variably along the stream banks, whereas a net deposition of approximately 8 cm occurred rather uniformly over the midstream except at a constriction of the channel where 27 cm of sediment was lost. Scour and sediment level changes were less extensive during other times of the year, but the top layer of sediment clearly was a consistently highly dynamic area of the stream.

Data on mean depth of scour (Table 1) and detritus storage (Fig. 1) were used to determine the amount of detritus exposed to the surface during each time period. Large quantities were exposed over the year, ranging from 0.4 kg/m^2 during October to January to 1.6 kg/m^2 during August to October (Table 2). Because of the size class distribution of stored detritus (Fig. 1), most material exposed was large wood and 1–8 mm particles.

Detritus processing and transport

Freshly fallen buried leaves were processed slowly compared with leaves on the sediment surface, a mean of 25% of initial AFDM of the three species still remaining after 15 mo (Fig. 3). Leaves typically were blackened and a hydrogen sulfide odor occasionally was evident. Processing coefficients ($-k$/d) were 0.005 for black gum and 0.003 for red maple and water ash; the coefficients were not statistically different (ANCOVA; $P>0.05$).

Percent reduction of detritus >0.053 mm in the embedded cores was not significantly different between HOC and LOC areas (t-test; $P>0.05$) so data from all cores for a given time period were pooled. Significant net processing (i.e. mass reduction was significantly different from zero; t-test, $P<0.05$) occurred during each time period, though not necessarily for all detritus size classes (Table 3). Processing rates of all size classes combined were most rapid from January to March when mass reduction was 19% compared with 8–9% during the other time periods. The processing coefficient for all detritus combined in the cores during January to March was 0.003, corresponding to a 240-d processing half-time (i.e. time for one-half

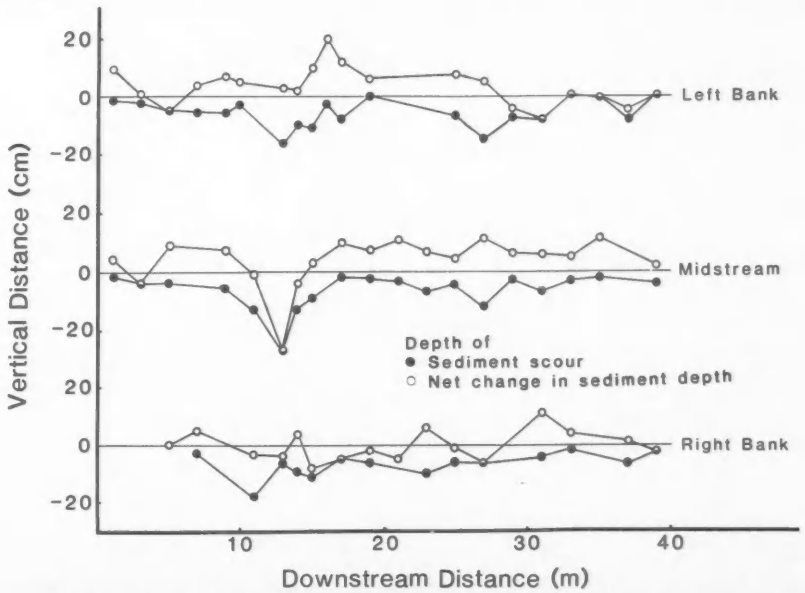

FIG. 2. Mean sediment scour depth and mean net change in sediment depth from August to October (which includes the period of high discharge due to rainfall from Hurricane Gloria).

TABLE 2. Mass of detritus (AFDM; g/m^2) exposed to the surface by sediment scouring. >8 refers to the detritus fraction with wood >8 mm removed.

	Size class (mm)					
Time period	0.053–0.15	0.15–1	1–8	>8	Wood >8	Total
Aug.–Oct.	162	367	498	45	522	1594
Oct.–Jan.	30	69	125	8	161	393
Jan.–May	58	144	247	15	427	891
May–Aug.	83	197	276	16	377	948

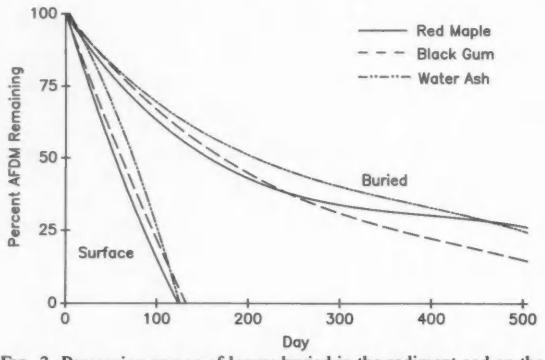

FIG. 3. Processing curves of leaves buried in the sediment and on the surface of Buzzards Branch. Data for leaves on the channel surface from L. A. Smock (unpubl. data). Day 0 is 3 December 1984.

TABLE 3. Mean net processing (± 1 SE) of different size classes of buried detritus over 72–78 d. * = mass reduction significantly different from 0 ($P<0.05$).

	Percent reduction of AFDM		
Size class (mm)	Sept.–Nov.	Jan.–Mar.	Apr.–June
0.053–0.15	21 (5)*	6 (3)*	7 (5)
0.15–1	11 (2)*	18 (3)*	9 (3)*
1–8	1 (12)	24 (10)*	7 (13)
>8	14 (2)*	13 (3)*	11 (3)*

of the original detritus to be processed to <0.053 mm). Processing coefficients for the September–November and April–June periods were 0.001, corresponding to a 555-d half-time.

The mass of detritus of each size class processed within, or transported into or out of the sediment was calculated using equation (1), the data on detritus storage (Fig. 1) and processing rates of specific size classes of detritus. Processing rates of large wood were assumed negligible over the short time periods of the processing studies; hence transport of this material can be determined solely from temporal changes in storage (Fig. 1).

From August to October, when two heavy rainfalls occurred, there was a net release of 612 g/m^2 from the sediment, resulting in a 27% reduction in stored detritus (excluding large wood). Nearly all of this reduction was particles of size 0.15–8 mm (Fig. 4). Processing accounted for an additional loss of 332 g/m^2, primarily particles <1 mm. Thus the total AFDM loss from the hyporheic zone from August to October was 944 g/m^2.

Net transport during October to January was into the sediment (i.e. burial) and totalled 677 g/m^2. Most of this was particles of size 0.15–8 mm (Fig. 4). Loss due to processing during this time was 664 g/m^2 and was primarily particles 1–8 mm. The result was a net increase of 13 g/m^2 of detritus in the hyporheic zone over these months.

From January to May some net burial of particles of size 0.053–1 mm occurred, but there was no significant net input of larger particles (Fig. 4). This was likely a result of increased availability of FPOM relative to CPOM on the sediment surface. Total net transport was 305 g/m^2 into the sediment. At the same time, processing reduced storage by 180 g/m^2, resulting in a net gain of 125 g/m^2.

The amount of detritus exposed during sediment scouring (Table 2) and the amount of detritus transported out of the sediment from August to October (Fig. 4) were used to calculate the percent of exposed detritus that was transported out of the sediment and then reburied during that time (100% − (amount transported out of the sediment/amount exposed)(100%)). Detritus not reburied represents previously buried material that, once released from the sediment, remained on the channel surface or was transported to downstream areas or to the floodplain. Little detritus in three size classes was reburied: 0.053–0.15 mm (14% reburied), 0.15–1 mm (8%), and >8 mm (0%). About 65% of particles in the 1–8 mm size class, however, was reburied.

Discussion

The hyporheic zone is an important component of organic matter dynamics in Buzzards Branch. Sediment instability, in terms of both scour and deposition, is a key factor affecting storage, processing, and transport of buried detritus through its effect on burial and release of detritus and the chemical environment (particularly dissolved oxygen). High spatial and temporal variability in sediment movement resulted in highly variable detritus storage and movement in the channel. Hyporheic invertebrates are affected by this variability (Strommer and Smock 1989).

In Buzzards Branch, large quantities of detritus were buried in the sandy sediment, the annual mean of 4.8 kg/m^2 of organic matter stored in the subsurface being approximately an order of magnitude greater than that found on the stream's surface (Smock et al. 1989; Smock 1990). Hyporheic zone storage also was 3–20 times higher than surface storage reported for higher-gradient headwater streams (e.g. Minshall et al. 1983). Few measurements of detritus storage in the hyporheic zone of other streams have been made, but several studies suggest much greater subsurface than surface storage (Herbst 1979; Cummins et al. 1983). Streams with loose, shifting sediment, such as Buzzards Branch, have up to several hundred times more buried detritus than high-gradient streams with coarse sediments (Godbout and Hynes 1982; Cummins et al. 1983).

Changes in the stored pool of hyporheic detritus occur both through processing and transport. Processing continuously reduces the amount of detritus, although at fluctuating rates. Transport, which may be into or out of the hyporheic zone, is highly dependent on timing of leaf litter inputs into the stream and the stream's hydrologic and spatially variable geomorphic characteristics.

The large pool of buried detritus in Buzzards Branch was maintained by continual burial in the shifting top sand, only rare episodic loss of detritus stored deep in the sediment and low processing rates. The latter was especially important given the slow processing of wood, which comprised the majority of

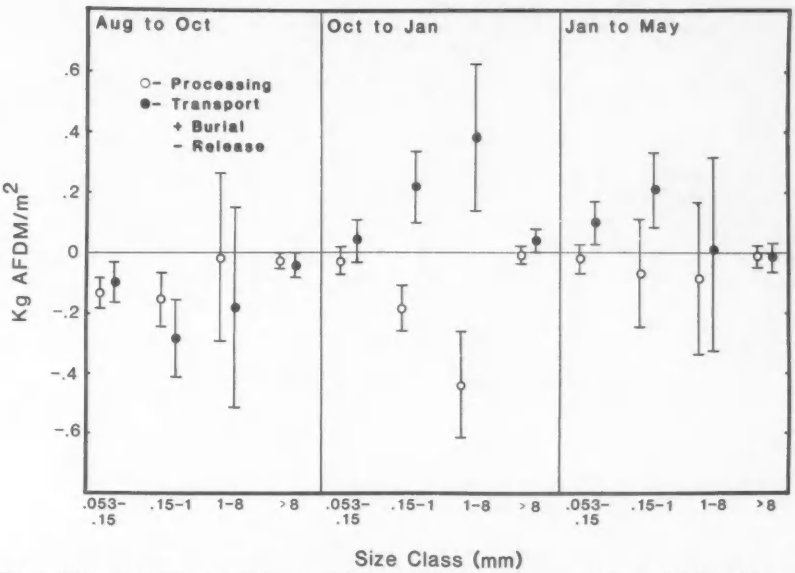

FIG. 4. Mean net processing and net transport of different size classes of buried detritus. Positive numbers indicate an increase in storage. Error bars = ±1 SE.

buried detritus (Fig. 1) both as particles >8 mm and also as a major component of the 1–8 mm fraction. Processing rates of leaves buried in the sediment also were very slow, similar to the results of Herbst (1980) and Rounick and Winterbourn (1983), and were much slower than rates for leaves on the sediment surface of Buzzards Branch (Fig. 3). The 6–24% mass reduction of buried FPOM over 72–78 d was far less than the 33–63% reduction found by Mattingly (1986) over a similar time period for FPOM processed on the surface of an Oregon stream. Burial of the detritus in our study was the likely reason for much of the difference in percent mass loss between our study and that of Mattingly (1986).

A number of factors probably caused the slower processing of buried leaves compared with leaves on the surface, including reduced mechanical abrasion and low dissolved oxygen concentrations. Anoxic conditions, which were prevalent throughout much of the hyporheic zone (Metzler 1987; Strommer and Smock 1989), significantly decrease the rate of activity of hyphomycete fungi (Holt and Jones 1983), the major microbial decomposers of detritus in streams (Cummins and Klug 1979). Also, shredding invertebrates were rare in the hyporheic zone (Metzler 1987; Strommer and Smock 1989), although they were common in detritus on the surface (Roeding and Smock 1989). Shredders probably were limited in the subsurface sediments by low oxygen concentrations, unsuitable substrate and a lower palatability of buried versus surface leaves (Herbst 1980).

Changes in nutritional quality of detritus, although not measured, also may have affected processing rates. Nutritional quality probably was at a peak during January to March, following the large pulse of autumnal input of fresh leaves. Slower processing noted later in the year likely reflected an increase in refractory carbon in the majority of detritus present in the sediment. This may have been especially true of particles 1–8 mm in size, much of which was leaf litter during the early winter months and which had a 24% mass loss during that period compared with 1–7% mass losses from April to June when these particles consisted primarily of wood fragments (Table 3). The differences in processing rates were not caused by higher water temperatures increasing microbial activity, since fastest processing occurred when water temperature was lowest.

Besides processing, burial and release of detritus were important in determining fluctuations in storage in the hyporheic zone over the year. High discharge and scour associated with heavy rain in late September had a definite effect on the transport component of detrital dynamics, scour removing 612 g/m^2 of detritus from the sediment during that time. Autumnal inputs of detritus to the stream did not return buried storage to prestorm levels; hence the effects of the storm on the amount of stored detritus were long-lasting. In addition, the storm also significantly altered the relative abundance of different size fractions of buried detritus. The proportional abundance of large wood increased and that of smaller-sized particles decreased (Fig. 1), probably affecting rates of microbial and macroinvertebrate utilization of detritus.

Most of the 0.053–1 mm particles and the nonwoody detritus >8 mm that was exposed by scour during August to October was not reburied, but rather must have been transported downstream or settled onto the floodplain. Storms thus made available a large quantity of subsurface detritus, in various stages of decay, to other areas of the stream ecosystem.

A large net increase in subsurface detritus storage was expected from October to January due to input of leaf litter to the channel during autumnal leaf fall. Instead, burial was nearly entirely offset by losses to processing (Fig. 4). Lack of heavy rainfall shortly after leaf fall, and the resulting little scour and deposition (Table 1), may have reduced input of detritus to the hyporheic zone. Given an autumnal leaf fall of 321 g/m^2 (Smock 1990), correcting for loss to processing, and using our estimate of detritus burial during October to January, 25% of direct leaf fall to the channel became buried. This is lower than Herbst's (1979) estimate of 46% for a low-gradient stream with a loose substrate, but no doubt is subject to considerable annual vari-

ation depending on the extent and timing of spates. We suspect that spates after leaf fall are critical for initially burying leaves. Replenishment of buried detritus probably was not extensive during our study because the number and magnitude of spates was lower than usual during the critical months immediately following leaf fall.

Subsurface detritus storage can be separated into two types: shallow and deep. Shallow storage includes only the top several centimetres of sediment and involves detritus that is frequently buried and released due to nearly constant movement of the topmost sediment layer. This effectively mixes detritus deposited on the sediment surface with that in the upper layer of sediment. Dissolved oxygen concentrations in the top sediment, while lower than on the surface (Strommer and Smock 1989), probably are not sufficiently low to significantly affect microbial and invertebrate activity.

Deep detritus storage encompasses sediment below the shallow layer that is scoured only during relatively rare events, dependent on storms such as that associated with Hurricane Gloria in this study. Both particulate and dissolved organic carbon in deep storage may not be released for years both because of physical entrainment and because of the much slower processing rates mainly due to the often anaerobic conditions.

Hyporheic storage, and especially deep storage, greatly reduce downstream carbon transport. This is particularly important in sand-bottomed streams where surface retention of detritus is relatively inefficient, particularly during spates (Smock et al. 1989). Hyporheic storage thus affects carbon spiralling lengths (Newbold et al. 1982), both the transport and biological utilization components of spiralling being decreased relative to those for surface detritus.

Microbial and invertebrate utilization of buried detritus, though slower than on the surface, is potentially important to overall stream metabolism (e.g. Grimm and Fisher 1984) and for the production of dissolved organic carbon and release of nutrients (Crocker and Meyer 1987). Near continual release of both particulate and dissolved carbon from shallow storage may help to temporally stabilize energy flow in the stream. Episodic release from deep storage makes available a large quantity of a new source of carbon to the stream surface, potentially at times when surface supplies may be scarce. Given the large quantity of detritus stored in the hyporheic of Buzzards Branch compared with that on the sediment surface, the subsurface compartment no doubt is an important component of detritus dynamics of this stream.

Acknowledgements

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Experimental Harvesting of Cyclic Stocks in the Face of Alternative Recruitment Hypotheses

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Cyclic fluctuations in year-class abundance have been recorded for several fish populations. Historical patterns are generally consistent with several hypotheses about underlying mechanisms, which involve (a) strong density dependence or (b) environmental forcing. Optimal harvesting policies differ depending on which hypothesis is deemed true. Not only does the harvesting policy affect the amount of catch taken, but it can strongly affect our ability to discriminate between alternative hypotheses. Fully-adaptive feedback policies, which explicitly account for the information content of harvest controls, were computed with dynamic progamming for some model prototypes of the problem. Results indicate that deliberate experimentation with escapement levels, oriented to reduce the uncertainty, may be worthwhile under some conditions. In most cases, however, optimal passive policies (in which learning occurs passively) were a good approximation to actively adaptive policies. The optimal passive controls for maximizing a risk-neutral objective, such as total catch, were generally very informative. Although passive and active controls markedly differed in some cases, expected discounted yields under the two types of policies were very similar (differences less than 2%). The extreme risk-averse presciption of managing a stock according to the more pessimistic recruitment model may lead to considerable yield losses.

Les fluctuations cycliques de l'abondance des classes annuelles ont été enregistrées chez plusieurs populations de poissons. Les tendances observées concordent dans l'ensemble avec plusieurs hypothèses concernant les mécanismes sous-jacents, qui appellent (a) une forte dépendance à l'égard de la densité ou (b) l'influence des forces environnementales. Les politiques optimales de prélèvement diffèrent selon l'hypothèse retenue. Non seulement la politique de prélèvement affecte-t-elle la quantité des captures, mais elle peut modifier fortement notre aptitude à faire la différence entre les deux hypothèses. Les politiques fondées sur une rétroaction entièrement adaptative, qui rendent compte de façon explicite de la quantité d'information fournie par les contrôles du prélèvement, ont été calculées par programmation dynamique pour certains prototypes modèles du problème. Les résultats indiquent que l'expérimentation délibérée sur les niveaux des échappées, orientée de façon à réduire les incertitudes, peut se justifier dans certaines conditions. Dans la plupart des cas, toutefois, les politiques passives optimales (dans lesquelles l'apprentissage se fait de façon passive) constituent une bonne approximation des politiques activement adaptatives. Les contrôles passifs optimaux visant à maximiser un objectif à risque neutre, comme le total des captures, sont généralement très informatifs. Bien que les contrôles actifs et passifs se soient révélés nettement différents dans certains cas, les rendements actualisés prévus selon les deux types de politiques étaient très similaires (différences de moins de 2 %). L'usage extrêmement risqué qui consiste à gérer un stock selon le modèle pessimiste du recrutement peut amener à des pertes de rendement considérables.

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In this article we address the question of how to manage a fish population with a history of apparent cyclical changes in recruitment, which are consistent with two alternative hypotheses: (1) the recruitment trend is induced by changes in the spawning biomass, which negatively affects juvenile production, and (2) the recruitment trend is driven by an extrinsic cycle. The relative importance of density-dependent mechanisms versus extrinsic factors in driving recruitment fluctuations cannot be assessed from the information usually available. Environmental cycles of intermediate periods superimposed on the stock production dynamics can obscure any underlying relationship between recruitment and spawning biomass (Walters 1987; Walters and Collie 1988; Armstrong and Shelton 1988).

Management decisions are specially problematic here because the alternative models of population regulation dictate radically different harvesting strategies. Adjusting spawning targets in response to anticipated environmental conditions would be adequate if juvenile survival rates could be unequivocally linked to the variables in question. Unfortunately, this is seldom the case. A number of studies have shown significant correlation between estimates of population abundance and some extrinsic variable exhibiting periodic or quasiperiodic behavior (Cushing 1982; Southward et al. 1975; Caddy 1979; Mysak 1986; Johnson et al. 1986; Koslow et al. 1987). Yet, causal relationships cannot be inferred from that type of evidence. In fact, in most cases where cyclic fluctuations have

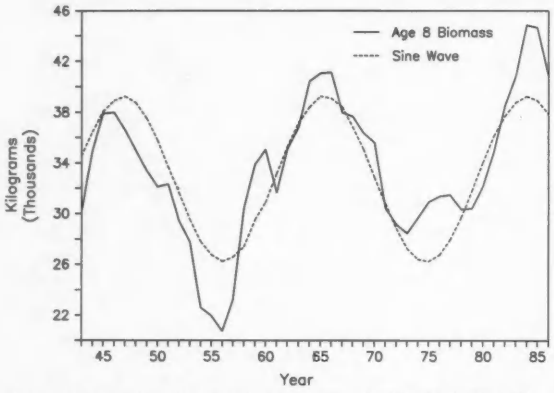

FIG. 1. Fluctuations in year-class abundance for Pacific halibut (Deriso et al. 1987).

been recorded, the historical time series has proved to be consistent with several hypotheses involving biological feedback control or environmental effects. Examples are the Dungeness crab in Northern California (Botsford et al. 1989) and the Pacific halibut (Deriso et al. 1986). Spawning biomass and juvenile production estimates of Pacific halibut exhibit opposite trends for the last fifty years, which suggests density-dependent regulation (Deriso 1985a). Recruitment also exhibits a cyclic trend (Fig. 1), which is consistent with environmental forcing. These hypotheses are in fact the extremes of a continuum of plausible explanations involving various degrees of density dependence and environmental contrast.

Alternative models consistent with historical records usually make different predictions over some range of management choices or system states. Thus, the propagation of the uncertainty over time depends on the harvesting policy selected (Walters 1986). The confounding of environmental and stock-size effects is maximal when the spawning biomass is allowed to cycle in response to recruitment fluctuations, in such a way that the stock rebuilds by the time environmental conditions have deteriorated. Burkenroad (1951) suggested that a controlled fishery experiment would help discern among alternative causes for the fluctuations in abundance of Pacific halibut. Deriso et al. (1986) noted that forcing the Pacific halibut stock out of phase with the postulated extrinsic cycle would provide the most information for testing the density-dependence versus environmental-forcing hypotheses. Two types of experimental actions can be envisioned: (1) forcing the spawning-stock down to a level close to the optimum under the hypothesis of density dependence when unfavorable conditions are anticipated, or (2) allowing large escapement levels when a favorable environment is expected. The first type of action may entail high risks of recruitment collapse in case the environmental hypothesis proves valid. However, the actual trade-offs between short-term costs and future benefits derived from learning are difficult to evaluate. Furthermore, what is intuitively the best experiment in terms of hypothesis testing may not be the best compromise between short- and long-term management objectives.

In order to formally address these questions we must evaluate whether the costs incurred by experimenting with the fishery are exceeded by the expected long-term derived benefits and, if they are, when and how is it worthwhile to experiment. This implies solving a high-dimensional optimization problem: "best" management decisions will depend on several state variables, including those that describe the stock and environmental conditions, and the credibility of the alternative hypotheses. Computing optimal policies using realistic models of age-structured populations is not possible with the methodologies available. Our approach was, instead, to construct some extremely simplified prototypes of the management problem, for which optimal harvesting policies can effectively be computed. Results derived from these simple prototypes can provide guidance with which to approach more complex realistic situations.

Each prototype represents a hypothetical fish stock whose historical series of stock–recruitment data exhibit: (1) a negative relationship between recruitment and spawning biomass, consistent with a dome-shaped stock–recruitment function, and (2) a cyclic trend in recruitment, consistent with environmental forcing. We assume that both the spawning biomass and recruitment are observed without error, and that parameters of the alternative stock–recuitment relationships are all known but which model is true is unknown.

We contrast the behavior of two different types of policies: actively adaptive and passively adaptive (Walters 1986). Actively adaptive policies may call for deliberate experimentation with spawning quotas in order to reduce the uncertainty about the system dynamics. In computing these policies, we explicitly represent how the probability assigned to the alternative models propagates through time as a function of different management choices. In contrast, passive policies are computed ignoring the fact that alternative actions have different informative value; learning will nevertheless occur, but passively. We used a dynamic programming algorithm similar to that developed by Walters (1981). Our prototypes and harvesting policies are more complex than Walters's, because additional variables are needed here to describe the system. Also, previous analyses assume that system responses to management interventions are observed without lags. Here we explore the effects of incorporating lags in the learning process, which further increases the dimensions of the optimization problem.

We first describe the behavior of risk-neutral policies computed by maximizing expected discounted yields. Experimental choices can be risky, especially if the more pessimistic alternative turns out to be true. In order to address those concerns we also computed optimal policies for a risk-averse objective, such as the expected sum of discounted logarithms of catches. The performance of risk- neutral, risk-averse, and constant harvest rate policies is contrasted.

Confounding of Environmental and Stock-Size Effects, and Management Implications

Many mechanisms are responsible for the common confounding between environmental and stock-size effects in cyclic populations. Suppose that an environmental trend induces a cycle in juvenile production. If the period of the extrinsic cycle and the life-history parameters are such that, for a given harvesting history, the spawning population tracks the environment with a delay of about half the period of oscillations, opposite trends between population abundance and recruitment level will result, providing false evidence of density-dependent regulation. Maximum biases have been shown to occur when the period of the extrinsic cycle is twice the mean age of the spawning population (Armstrong and Shelton 1988). Cycles of longer or shorter periods would produce a periodic pattern in the residuals of a stock–recruitment fit. This could not be unequivocally attributed to environmental forcing since cyclic residuals can

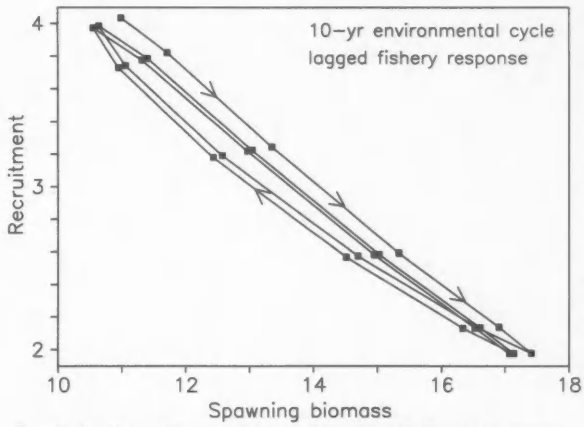

FIG. 2. Spurious evidence of density-dependence in the stock–recruitment relationship when the recruitment dynamics is driven by an extrinsic 10-yr cycle, and a policy that responded with a lag to changes in stock abundance is applied. The time series of stock–recruitment data was generated using the delay-difference model (1) for a stock with low average productivity (see text for details).

also be an artifact resulting from, among other things, misspecification of the age-dependent maturity schedules or errors in the ageing process. Bergh and Getz (1988) showed for delay-difference models that such a pattern can be caused by the use of an incorrect lag coefficient.

Density-dependent mechanisms inducing over-compensation can cause periodic fluctuations in recruitment even if the deterministic system is intrinsically stable and environmental disturbances are serially uncorrelated. Allen and McGlade (1986) showed that feedback responses from fishermen may exacerbate the effects of a random environment by generating cycles of fish population boom and bust despite the intrinsic stability of the system. Fishing effort usually responds with some lag to changes in stock abundance, which can also contribute to generating a cycle (Botsford et al. 1983; Caddy and Gulland 1983).

The problem can be best illustrated by means of a simple prototype. Consider the time series of stock–recruitment points in Fig. 2. These were generated using a nonstationary model, in which year-class abundance is largely determined by an extrinsic cyclic factor. The dynamics of the population was represented by a simple delay-difference model, of the form

$$(1)\quad N_{t+1} = lS_t + R_{t+1},$$

where N_t denotes the abundance of the adult population in year t, S_t is the stock left after a short harvesting season (escapement), which takes place at the beginning of the year, preceding the reproductive season, l is survival from natural mortality, and R_{t+1} is recruitment of young fish in year $t + 1$. As discussed in Parma (1990b), the equation above can be alternatively used to model a population measured in biomass units. In that case, the coefficient l (approximately) represents net growth (growth minus natural mortality). For the illustration we used $l = 1$ and assumed that knife-edge recruitment occurred at age 2. Environmental trends were incorporated as a time shift in one of the parameters of a Ricker (1954) stock–recruitment function, such that

$$(2)\quad R_{t+1} = S_{t-1}\exp\{a_{t-1} - bS_{t-1}\},$$

where a_t is a time-varying parameter controlling density-independent effects, and $1/b$ is the spawning level at which recruitment peaks. The parameter a_t followed a sinusoidal trend with a period of 10 yr, and maximum and minimum values of -0.386 and -1.20. A policy in which harvest rates were adjusted to changes in stock abundance was applied; harvest rates oscillated between 0.1 and 0.25, tracking the cycle in biomass with a lag of 3 yr.

Suppose now that spawning targets for this hypothetical stock had to be chosen on the basis of the stock–recruitment data in Fig. 2. A standard stock–recruitment analysis would result in a far more productive relationship than the one used to generate the data. The dashed lines in Fig. 3a correspond to the true stock–recruitment functions (upper curve represents the most favorable environment in the cycle and lower curve the least favorable one) used to simulate the trajectory; the solid curve is the Ricker function fitted to the "observed" data. On the other hand, the cycle in year-class abundance would suggest a hypothesis of extrinsic regulation, even though no specific environmental forcing factors were identified. The relative importance of environmental and stock-size effects cannot be assessed from the historical records.

Management decisions in a situation like the one described would have to be made in the face of two radically different hypotheses. We will refer to the model that represents the density-dependence hypothesis as model 1, and to the model that represents the environmental-forcing hypothesis as model 2. These alternative models imply very different stock productivities. Model 1 corresponds to a more optimistic hypothesis which calls for exploitation rates higher than those that are optimal under model 2. Managing the fishery according to model 1 would put the stock at risk if model 2 turned out to be true. On the other hand, a conservative strategy based on model 2 might lead to considerable yield losses if model 1 were true.

Some Simple Prototypes

We developed three prototypes of the management problem that, although extremely simplified, capture the essentials of decision making in the face of two alternative hypotheses. These prototypes were used in the policy analysis.

In the three prototypes, the dynamics of the adult stock measured in units of biomass is given by equation (1). The coefficient l was always set to 1, implying that growth and natural mortality balanced when averaged across age classes. We assume in each prototype that two alternative hypotheses about the stock–recruitment relationship (SRR) exist, of which only one is true but the decision maker does not known which one. The alternative hypothesis are given by alternative stock–recruitment functions, denoted as F^1 for model 1, the density-dependence hypothesis, and F^2 for model 2, the environmental-forcing hypothesis. Specifically, the SRR under model m is given by

$$R_{t+1} = F^m(S_{t-k})e^{\sigma Z_{t-k}},$$

where $k + 1$ is the age at which fish recruit into the adult stock, and $\{\sigma Z_t\}$ is a sequence of independent, normally distributed random variables with mean 0 and variance σ^2. The existence of an extrinsic driving force was incorporated as a sinusoidal trend in the value of the parameters of F^2. We will use an index $i_t \in \{1,\ldots,w\}$ to represent the environmental conditions prevailing at time t, such that if $i_t = 1$, then $i_{t+1} = 2$, $i_{t+2} = 3$, etc., and $i_{t+w} = i_t$, w being the period of the environmental

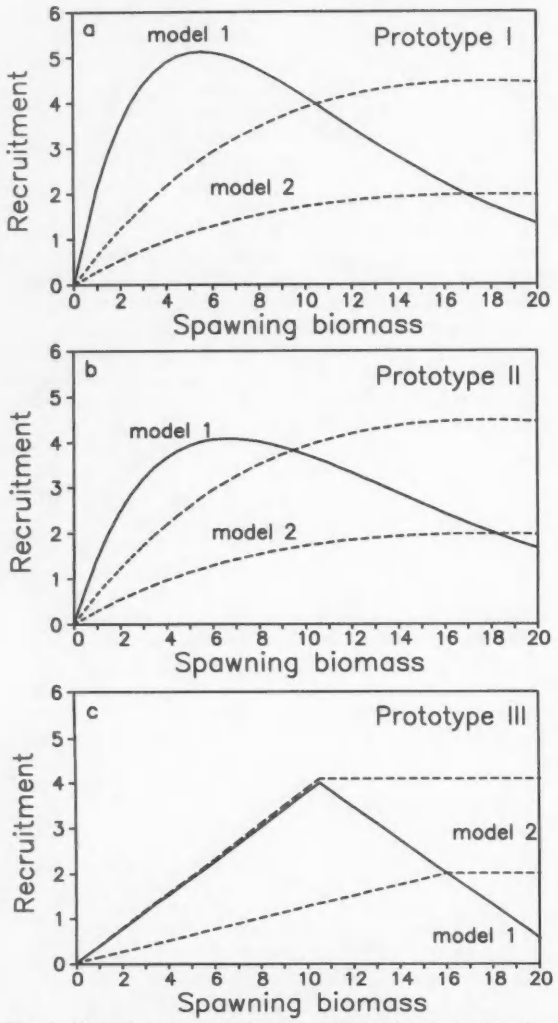

FIG. 3. Alternative stock–recruitment models used in the optimization trials. In the three figures (a, b, and c), solid lines represent the stock–recruitment functions for model 1, the density-dependence hypothesis. Dashed lines represent model 2, the environmental-forcing hypothesis; the upper curve corresponds to the most favorable environment in the cycle and the lower to the worst. The stock–environment function of model 2 in prototypes I and II was the one used to generate the trajectory in Fig. 2. Model I in prototype I was obtained by fitting a Ricker (1954) function to the stock–recruitment data in Fig. 2. A less productive Ricker function was used for prototype II. Alternative models in prototype III are also consistent with the stock–recruitment data in Fig. 2. Maximum recruitment level in model 2 follows a 10-yr cycle with extremes equal to 4 and 2.

cycle (assumed to be an integer); the most favorable environmental conditions in the cycle will be assigned a value of $i = 1$. The fact that F^2 is conditional on i will be denoted as $F^2(S|i)$. In our computations we always used $w = 10$. We assumed that recruitment occurred at age one (lag coefficient $k = 0$) for most of the optimization trials, although a limited number of policy computations were performed with $k = 1$.

The specific stock–recruitment functions for the three prototypes are shown in Fig. 3. In the case of model 2 (dashed lines), only the functions corresponding to the extreme environmental conditions (i.e. $F^2(S|1)$ and $F^2(S|6)$ for an environmental cycle of period $w = 10$) are graphed. In the first two prototypes, both stock–recruitment functions (1 and 2) correspond to Ricker models. The parameter a in model 2 was assumed to follow a sinusoidal trend, such as was done before (see equation (2)), with maximum and minimum values given by a_{max} and a_{min}. Parameter values were constant in model 1.

The stock–recruitment functions used in Prototype I arose from the illustration in Fig. 2. Parameter values for model 2 are: $a_{max} = -0.386$, $a_{min} = -1.20$, and $b = 0.056$. Parameter values for model 1, obtained from the least-squares fitting of a Ricker function to data in Fig. 2, are $a = 0.925$ and $b = 0.179$.

We wanted to consider two other prototypes that have some different properties. The density-dependent model in prototype I has a very steep slope at the origin; indeed, that productivity level would hardly be credible on the basis of the restricted range of spawning-stock abundances used in the fitting. This reflects a limitation of the Ricker function itself: the more negative the slope on the right-hand side of the curve, the steeper its slope at the origin. In a second prototype (Fig. 3b), the productivity level of model 1 was arbitrarily lowered ($a = 0.5$ and $b = 0.15$) while model 2 was not modified. Prototype III (Fig. 3c) is even more conservative in this respect: predicted recruitment levels never exceed the "observed" values and, in fact, they sharply decline when the population abundance is lowered below its "historical" range. In addition, here the recruitment function of model 2 reaches its maximum value at an escapement level distinctly higher when unfavorable conditions are anticipated than when a favorable environment is expected.

Two levels of process noise were used in all the optimization trials: $\sigma = 0.3$ and $\sigma = 0.5$. These values were chosen arbitrarily. The same value of σ was used for both models 1 and 2. In the case of $\sigma = 0.5$, the values of the a parameter were adjusted from those given before so that the expected value of recruitment as a function of spawning-stock abundance (a log-normal random variable) would be unaffected by the increase in σ. Since the expected value of $\exp\{Z\}$, where Z is normally distributed with mean zero and variance σ^2 equals $\exp\{\sigma^2/2\}$, the adjusted values of a were set equal to $a + 0.3^2/2 - 0.5^2/2$.

Formulation of the Optimization Problem and Computational Scheme

Walters (1981) presented a dynamic programming formulation for designing optimal policies when there are two alternative hypotheses for the SRR. We summarize here the basics of that approach while adapting it to our specific prototypes. Some differences in the optimization algorithms used in the analyses here will be opportunely indicated.

The system at time t is described by a number of state variables, namely, the recruitment level R_t, the sequence of past spawning levels needed to compute future recruitment probabilities, and the environmental index i_t. Future recruitment probabilities conditional on each hypothesis are computed using $F^1(S)\exp\{\sigma Z\}$ for model 1 and $F^2(S|i)\exp\{\sigma Z\}$ for model 2. The number of past spawning levels required as state variables is equal to k, specifically $\{S_{t-1}, \ldots, S_{t-k}\}$ for $k \geq 1$. When $k = 0$, although only $N_t = R_t + lS_{t-1}$ is needed, we found it convenient for computational reasons to use the pair R_t and S_{t-1}.

Clearly, the incorporation of lagged effects into the models entails an increase in the dimensions of the optimization problem. The dynamic programming equations developed in what follows are only valid for the cases of $k = 0$ and $k = 1$, as used in the optimization trials. Computing time required to determine an optimal policy increases enormously with the incorporation of each additional state variable. Also, the behavior of the policy becomes increasingly difficult to visualize since optimal decisions are a function of several state variables.

The performance of any given policy has to be evaluated across the two alternative models considered plausible in the hypothetical system, by weighing alternative population responses according to their credibility. The uncertainty of the decision maker about which of the two models "is true" is characterized by the subjective probability assigned to one of the hypotheses. This probability is expected to fluctuate over time as new fishery data become available and the decision maker learns about the recruitment dynamics. Therefore, it has to be incorporated as an additional state variable, together with the variables describing the population and environmental conditions. Bayes theorem can be used to represent its dynamics in a recursive format (Walters 1981), when the probabilities are updated each year in an objective manner. If P_t denotes the probability assigned to model 1 prior to the recruitment observation R_{t+1} made at time $t + 1$, the posterior probability P_{t+1} is then a function of R_{t+1} and the prior probability, namely

$$(3)\quad P_{t+1} = \frac{P_t\, p(R_{t+1}|1)}{P_t p(R_{t+1}|1) + (1-P_t)\, p(R_{t+1}|2)}\ ,$$

where $p(R_{t+1}|m)$ is the probability density function (pdf) of R_{t+1} when model m is true. Assuming that both spawning biomass and recruitment are observed without error, these conditional pdf's are given by

$$p(R_{t+1}|1) = \frac{1}{R_{t+1}}\,\varphi\left(\ln\left(\frac{R_{t+1}}{F^1(S_{t-k})}\right)\right) \text{ and}$$

$$p(R_{t+1}|2) = \frac{1}{R_{t+1}}\,\varphi\left(\ln\left(\frac{R_{t+1}}{F^2(S_{t-k}|i_{t-k})}\right)\right)\ ,$$

where $\varphi(\cdot)$ denotes a normal pdf with mean zero and variance σ^2 and S_{t-k} was the spawning stock at time $t-k$. The denominator in equation (3) is then the probability of an outcome equal to R_{t+1}, as assessed by the decision maker on the basis of restricting the range of possible SRR's to $F^1(S)\exp\{\sigma Z\}$ and $F^2(S|i_{t-k})\exp\{\sigma Z\}$ with respective assigned probabilities P_t and $1 - P_t$. We can see in the formulation above that the propagation of the uncertainty over time depends on the sequence of management decisions $\{S_t\}$. The information content of a particular S_t depends on how far apart $F^1(S_t)$ is from $F^2(S_t|i_t)$. The least informative escapement choice is that for which the two models make exact predictions, that is when $F^1(S_t) = F^2(S_t|i_t)$. The chances of discriminating between the two hypotheses thus increase when management leads to system states over which the alternative models make distinctive predictions.

Having described the state variables and their transitions, we can now provide a rigorous definition of the two classes of policies that we will analyze here. These policies correspond respectively to active adaptation and passive adaptation (Walters 1981, 1986; Ludwig and Walters 1982). In both, an optimal course of action is selected after evaluating the performance of all possible choices under the alternative models. The actions will produce information which will affect the future credibility of the alternative models. The effect of current decisions on future learning is taken into account in the case of active adaptation, and it is neglected when adaptation is passive. When the value of an action is computed in the first case, P_t is incorporated as a state variable with dynamics given by equation (3). In passive adaptation, instead, possible population responses are weighted according to the current credibility of the alternative models, assuming that P_t will stay unchanged in the future. P_t is still a state variable, but equation (3) is replaced by $P_{t+1} = P_t$. These policies have been referred to as "Bayes equivalent" (Mendelssohn 1980; Walters 1981) or "myopic Bayes" (Ludwig and Walters 1982). They would be optimal if no additional data were to be gathered in the future. Although future learning is ignored when evaluating different courses of actions, in reality, the credibility of the alternative models will change as new data become available. This process is known as passive adaptation.

The dynamic programming equation has to incorporate the two alternative models for the population dynamics, as well as their respective credibilities P_t and $1 - P_t$. We will assume that a sequence of harvesting decisions has to be made over a management horizon of T years, where T is arbitrarily large. Let π_t denote a finite-horizon policy, defined by a series of control laws to be followed from year t to year T. By control law we mean a decision rule that determines the escapement level S_t as a function of the state variables at time t. We define the value function J_t^m of any given policy π_t conditional on model m being true as the expected discounted sum of future revenues or utilities to be obtained in the remaining $T-t+1$ years of the management horizon when policy π_t is implemented and model m determines the dynamics of the population; this is

$$J_t^m(R_t, S_{t-1}, i_t|\pi_t) = U(C_t) + E\left[\sum_{j=t+1}^{T} \alpha^{j-t} U(C_j)|\pi_t\right],$$

where $C_j = F^m(S_{j-k-1}|i_{j-k-1})\exp\{\sigma Z_{j-k-1}\} + lS_{j-1} - S_j$ is the catch in period j, given environmental noise Z_{j-k-1}, $U(C)$ is a function of the catch or utility, recruitment age $k+1$ is either 1 or 2, α is a discount factor, i_t is the index for the environmental conditions at time t, and $E[\cdot]$ is the expectation of $(\cdot)$, which is taken across all possible environmental outcomes $\{Z_j\}$ for $j\in\{t-k,\ldots,T-k-1\}$. Notice that at current time-step t R_t and S_{t-1} are treated as arguments in the value function, and S_t is determined by policy π_t. When $U(C)$ is a linear function of the catch, resulting optimal policies are denoted "risk-neutral" (Deriso 1985b). More cautious policies, which assure a more stable catch supply, are derived by using a "risk-averse" utility such as the logarithm of the catch (Mendelssohn 1982; Deriso 1985b). We set $U(C) = C$ when computing risk-neutral policies, and $U(C) = \ln(C)$ when computing risk-averse policies. For each of the two models $m = 1$ and $m = 2$ there exists an optimal policy defined to be that which maximizes J_t^m.

If there is uncertainty about which model is true, the value function of any given policy π_t has to be evaluated across the two probable models. The optimal policy π_t^* then results from maximizing

$$J_t(R_t, S_{t-1}, P_t, i_t|\pi_t) = P_t J_t^1(R_t, S_{t-1}, i_t|\pi_t) + (1 - P_t)\, J_t^2(R_t, S_{t-1}, i_t \pi_t),$$

the weighted sum of the conditional value functions. Let the maximum value function, out of all possible value functions, be distinguished by an asterisk, so that

$$J_t^*(R_t, S_{t-1}, P_t, i_t) = \max_{\pi_t} J_t(R_t, S_{t-1}, P_t, i_t|\pi_t).$$

The recursive dynamic programming formulation of the equation above gives the value function at time t as the time-t reward $U(C_t)$ plus the weighted sum of the two expected discounted value functions at time $t + 1$, one conditional on model 1 being true and the other conditional on model 2. If N_t is the population size immediately prior to the harvest, the single-period optimization problem is to find the escapement level S_t^* that solves

$$J_t^*(R_t, S_{t-1}, P_t, i_t) = \max_{S_t \leq N_t} \{U(C_t) +$$

$$(4) \quad \alpha P_t E[J_{t+1}^1(F^1(S_{t-k})e^{\sigma Z}, S_t, P_{t+1}, i_{t+1})] +$$
$$\alpha (1 - P_t)E[J_{t+1}^2(F^2(S_{t-k}|i_{t-k})e^{\sigma Z}, S_t, P_{t+1}, i_{t+1})]\},$$

where the expectations are now computed with respect to the environmental outcome at time $t - k$ (the time subscript of Z has been omitted to simplify notation). Since at each time step the optimal decision depends on P_t, the latter becomes an argument of the conditional (model-specific) value functions J_{t+1}^1 and J_{t+1}^2. These conditional value functions represent the discounted sum of single-period rewards $U(C_j)$ to be expected if model 1 or 2 were respectively true but management decisions in each year $j \in \{t, \ldots, T\}$ were the optimal ones based on assigning a probability P_j to model 1. They satisfy the recursive equations

$$J_t^1(R_t, S_{t-1}, P_t, i_t) = U(N_t - S_t^*) +$$
$$\alpha E[J_{t+1}^1(F^1(S_{t-k})e^{\sigma Z}, S_t^*, P_{t+1}, i_{t+1})]$$
$$J_t^2(R_t, S_{t-1}, P_t, i_t) = U(N_t - S_t^*) +$$
$$\alpha E[J_{t+1}^2(F^2(S_{t-k}|i_{t-k})e^{\sigma Z}, S_t^*, P_{t+1}, i_{t+1})]$$

where S_t^* is the escapement level that maximizes (4). In our analyses, P_{t+1} was either given by (3) or was set equal to P_t, depending on whether the searched policy was actively or passively adaptive. More generally though, since P_{t+1} is a probability assigned by the decision maker, any arbitrary value between 0 and 1 can be chosen; of course, such subjective decision may not be consistent with scientific evidence.

We used a dynamic programming technique known as "value iteration" (Walters 1986) to compute the optimal policies. The value functions J_t^1 and J_t^2 are computed iteratively starting out with arbitrary end values $J^m{}_T$ (we used $J^m{}_T(R_T, S_{T-1}, P_T, i_T) = U(R_T + lS_{T-1})$) and proceeding backwards using the recursive equations above. The state variables are all discretized into finite grids. At each step in the backwards recursion, the maximization in expression (4) has to be numerically carried out for each combination of state variable values. This implies finding the optimal escapement S_t^* for each state of the system subject to the contraint $S_t^* \leq N_t$. Once S_t^* has been found, the conditional value functions J_t^1 and J_t^2 are separately updated. After a number of backward steps, the computed optimal policy becomes "stationary", that is, the functional dependence of S_t^* on the state variables is independent of t. This stationary policy is then optimal for any arbitrarily long management horizon. Convergence to the stationary policy was guaranteed in our numerical experiments by setting $\alpha < 1$.

The formulation above was the one used for computing the passively adaptive policies and corresponds to that in Walters (1981). In the case of actively adaptive policies a different algorithm was used. A major simplification, which was pointed out to us by C. J. Walters (pers. comm.), results from noticing that when P_{t+1} is updated by Bayes theorem equation (4) can be replaced by

$$J_t^*(R_t, S_{t-1}, P_t, i_t) = \max_{S_t \leq N_t} \{U(C_t) +$$

$$(5) \quad \alpha P_t E[J_{t+1}^*(F^1(S_{t-k})e^{\sigma Z}, S_t, P_{t+1}, i_{t+1})] +$$
$$\alpha(1 - P_t)E[J_{t+1}^*(F^2(S_{t-k}|i_{t-k})e^{\sigma Z}, S_t, P_{t+1}, i_{t+1})]\}.$$

The equivalence of the two formalisms is proved in Appendix A. Although not immediately apparent, equation (5) allows for a much more efficient algorithm than equation (4). Notice that the superscripts indicating models 1 and 2 in (4) have been replaced by a star, since a single value function is now involved. Equation (5) can be more simply written as

$$J_t^*(R_t, S_{t-1}, P_t, i_t) = \max_{S_t \leq N_t} \{U(C_t)$$
$$+ \alpha E[J_{t+1}^*(R_{t+1}, S_t, P_{t+1}, i+1)]\},$$

where the expectation is now taken with respect to R_{t+1}, whose pdf is as given in the denominator of (3). In other words, when P_t is updated by Bayes theorem, there is no need to compute model-specific value functions in order to evaluate a policy. Instead, the problem can be solved by computing a single value function, treating R as a random variable with pdf given as a mixture of the modei-specific pdf's.

The numerical scheme, whether based on equation (4) or (5), requires the computation of the expectations on the right-hand side of the recursive equations. In order to approximate those expected values we used interpolation schemes similar to those derived by Ludwig and Walters (1982). In these schemes, a continuous value function at time $t + 1$ (say J_{t+1}^* in equation (5)) is approximated by linear interpolation between the discrete grid points, for which the value has been already approximated in the previous step of the recursive sequence. The expected value of the resulting piece-wise linear function is then computed exactly. A logarithmic scale was used for R, with grid size equal to 40. Grid extremes R_{max} and R_{min} were chosen so that the area under the tail of the distribution of R_{t+1} did not exceed 0.05. The value of J_{t+1}^* for $R > R_{max}$ and for $R < R_{min}$ was approximated by its value at the upper and lower grid extremes, respectively. Escapement levels were discretized on a linear scale and they were not allowed to exceed $S = 20$. The state variable P was also discretized into a finite grid (grid size was set equal to 10). Since the grids for R and P have to be chosen independently, P_{t+1} and R_{t+1} cannot be forced to simultaneously fall on a mesh point of their respective grids. The actual value of J_{t+1}^* (or J_{t+1}^1 or J_{t+1}^2) for each R_{t+1} on a mesh point of the R grid was approximated by linear interpolation over the P dimension between its value at the two P levels bracketing the actual P_{t+1}. Preliminary optimization trials indicated that the qualitative behavior of the policies computed was not altered by further increasing the sizes of the grids.

Two discount factors were used in all the optimization trials: $\alpha = 0.95$ and $\alpha = 0.99$. We deliberately chose an extremely low discount rate ($\alpha = 0.99$) in order to favor actively adaptive behavior. The output from each optimization trial is a table containing the stationary optimal escapement level S^* for each combination of state variable values. In the case of $k = 0$ the state variables are N_t, P_t, and i_t. When $k = 1$ optimal escapements are also a function of S_{t-1}.

In order to compare the performance of alternative policies (e.g. actively versus passively adaptive) we computed the value of each policy as the expected total discounted yield over a 20-yr period across the two alternative models. Passive learning was allowed when computing the value of Bayes equivalent policies. We used the simplified algorithm involving a single value function in all cases except for constant harvest rate policies. In the latter, management actions were assumed inde-

pendent of P_t. Therefore, the conditional value functions for each given harvest rate were computed independently of P_t, and they were averaged a posteriori to give the policy value for each P_t level.

The assumption that environmental conditions, recruitment, and spawning-stock levels are observed without errors exaggerates the learning capability of the decision maker. Unfortunately, alternative approaches which have been developed to deal with measurement errors in the state variables (like those in Bar-Shalom and Tse 1976; Smith and Walters 1981) are not applicable here. Those methodologies are based on approximating the value function as a second order expansion around some nominal trajectory of state variables and controls. Their conclusions are thus valid only for small perturbations around the nominal trajectory. When the two alternative models imply radically different state dynamics, deviations from any nominal trajectory may be too big, rendering the validity of the approach doubtful.

Numerical Results

Risk-Neutral Policies

The behavior of optimal policies can be better interpreted by first graphically examining the three prototypes in Fig. 3 with regard to the information content of alternative management actions. Consider for example prototype I. For each environmental condition in the cycle (only the most and least favorable conditions are represented in the figure), there exist just a pair of stock–recruitment curves representing the alternative hypotheses. Predictions from these two functions are markedly distinct for the whole range of spawning-stock sizes, except for some intermediate segment around the size at which the curves intersect. We will refer to this loosely defined range of escapement levels for which the two models make similar predictions as the "uninformative region". In order to facilitate the discussion, we will represent the problem as a black and white picture in which management actions are either informative (when escapement levels are outside the uninformative region) or uninformative (when they are within). The uninformative region shifts cyclically following the environmental trend; therefore, decisions that are informative in a poor environment may be uninformative in a favorable one and vice versa. This simplified picture is common to the three prototypes. Prototype III has the widest uninformative region: predictions of the two SRR's under favorable environmental conditions coincide over the entire range of escapement levels below that producing maximal expected recruitment.

Optimal stationary policies for risk-neutral objectives are usually of the "bang-bang" variety. Here it is optimal to refrain from harvesting unless the population exceeds an optimal escapement target, in which case the stock should be harvested down to that target level. When $k = 0$, escapement targets are only a function of P_t and i_t. Optimal decision rules for actively adaptive policies were in some cases more complicated. Figure 4 illustrates the two basic types of decision rules obtained in the optimization trials. Optimal escapements for extreme environmental conditions ($i = 1$, the most favorable, and $i = 6$ the least) are shown as a function of stock size for five levels of P_t, the credibility of the density-dependence hypothesis. Results are for prototype I, with $\sigma = 0.3$, $k = 0$, and $\alpha = 0.99$. When $i = 6$, the control law is bang-bang for all levels of P_t, while when $i = 1$ it is not. Note the jump in the solid line for $P_t = 0.5$ and $i = 1$. There are two escapement targets

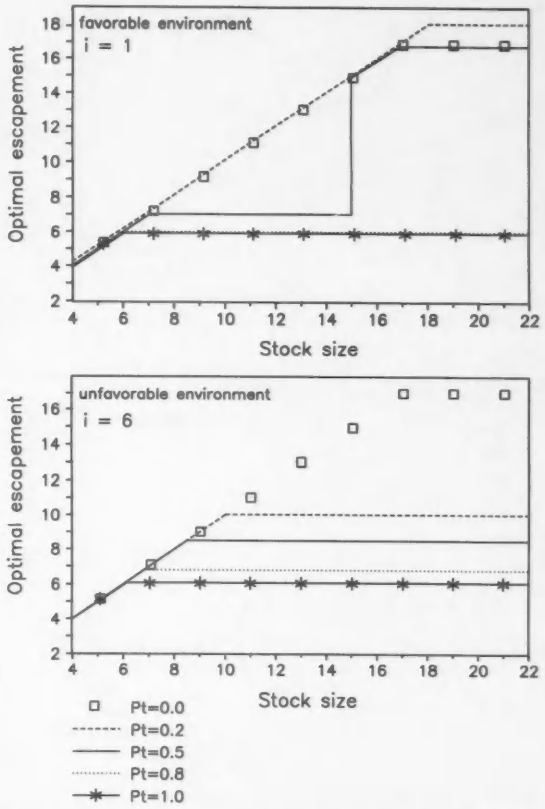

FIG. 4. Optimal risk-neutral controls for prototype I in Fig. 3 (with $k = 0$, $\sigma = 0.3$, $l = 1$, and $\alpha = 0.99$). Optimal escapements are plotted as a function of stock size for different levels of P_t, the probability assigned to the density-dependence hypotheses. Environmental conditions are the extreme in the 10-yr cycle postulated by the environmental-forcing hypothesis. Notice that for $i = 1$ and $P_t = 0.5$ there are two target escapements.

in this case, indicated respectively by the horizontal portions of the line.

We can now analyze how the optimal escapement targets vary in response to P_t and i_t. Figures 5 and 6 show policy feedback responses for prototypes I and III, respectively. For these results, the lag coefficient is $k = 0$, the process noise is $\sigma = 0.3$ and the discount factor is $\alpha = 0.99$. The figures contain a lot of information, which we will explain over the next several paragraphs, before discussing the specific results for each prototype. In each figure, results are presented for four environmental states in the 10-yr cycle; these are indicated by i, where $i = 1$ corresponds to the most productive SRR and $i = 6$ to the least. Intermediate states $i = 4$ and $i = 9$ correspond to periods of decreasing and increasing productivity, respectively. The left panels in the figures show the optimal escapements for both actively adaptive and Bayes equivalent policies as a function of the probability placed on model 2, the environmental-forcing hypothesis. The solid lines indicate the optimal escapement targets for the (bang-bang) Bayes equivalent policies, which shift smoothly with P_t, and are

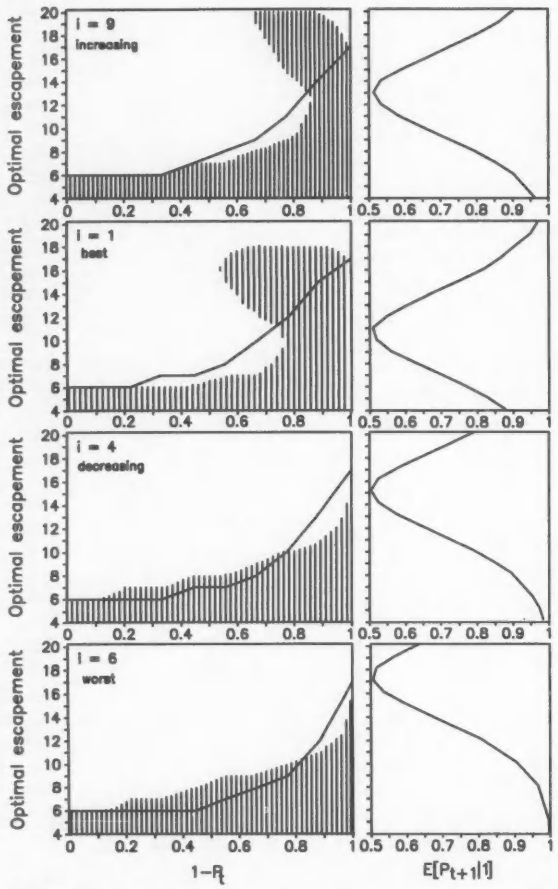

FIG. 5. Optimal escapement controls as a function of $1 - P_t$, the probability assigned to the environmental-forcing hypothesis. Results are for prototype I in Fig. 3 (with $\sigma = 0.3$; $k = 0$; $l = 1$ and $\alpha = 0.99$). Environmental conditions at time t are indicated by the index i ($i = 1$ is the most favorable environment in the 10-yr cycle and $i = 6$ the least). Passive policies are bang-bang with optimal escapement targets indicated by the solid lines. Actively adaptive optimal escapements for each P_t value correspond to the maximum feasible level within the shaded region. Panels on the right show a measure of the information content of alternative escapement levels: $E[P_{t+1}|1]$ on the x axes is the expected value of P_{t+1} when $P_t = 0.5$ and model 1 is true, if the escapement level on the y axes is used at time t. Values of $E[P_{t+1}|1]$ close to 0.5 indicate uninformative escapement levels.

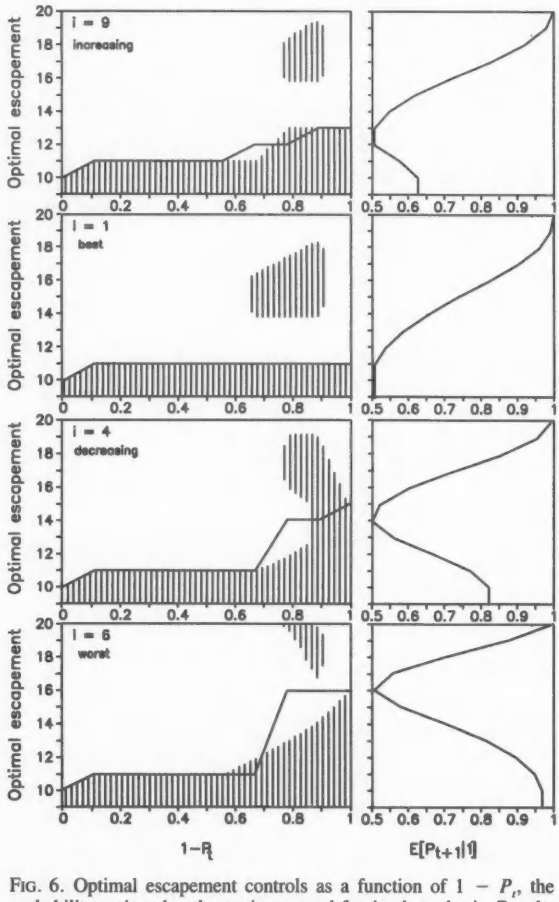

FIG. 6. Optimal escapement controls as a function of $1 - P_t$, the probability assigned to the environmental-forcing hypothesis. Results are for prototype III in Fig. 3 (with $\sigma = 0.3$; $k = 0$; $l = 1$ and $\alpha = 0.99$). Other details are as in Fig. 5.

always intermediate between the optimal levels for model 1 and those for model 2.

Actively adaptive policies were not always bang-bang, which complicates their graphic representation. For each probability P_t, the optimal active escapement corresponds to the maximum level within the shaded region that satisfies the constraint $N_t \geq S_t$. Discontinuities of the type described for Fig. 4 appear here as vertical discontinuities in the shaded region (see for instance $i = 9$ and $i = 1$ in Fig. 5) implying that the omitted escapement levels are never optimal. The optimal decision is then: (1) do not harvest when the stock is in the shaded region, and (2) harvest down to the shaded region when the stock is in the unshaded region. Consider for example Fig. 5 for $i = 9$ and $1 - P_t = 0.7$. If the stock size N_t exceeds 20, the optimal escapement equals 20; if $18 > N_t \geq 9$, the optimal escapement is 9, and if $20 \geq N_t \geq 18$ or $N_t < 9$, it is optimal to not harvest. When policy responses are bang-bang (like in Fig. 5 for $i = 6$), the optimal escapement target for each P_t is the maximum level in the shaded region.

In order to connect policy responses with the location of the uninformative regions, we computed for each environmental state a measure of the information content of alternative escapement levels. As a measure of the information content of a given S_t we chose $E[P_{t+1}|1]$, the expected value of the posterior probability placed on model 1 given that model 1 is true, S_t is the escapement choice, and the prior $P_t = 0.5$. Choosing model 1 as the true model and a prior equal to 0.5 was arbitrary. Panels on the right of the figures show the value of $E[P_{t+1}|1]$ (on the x axes) for each escapement level on the y axes. Values of $E[P_{t+1}|1]$ close to 0.5 indicate uninformative escapement levels and correspond to the point where the

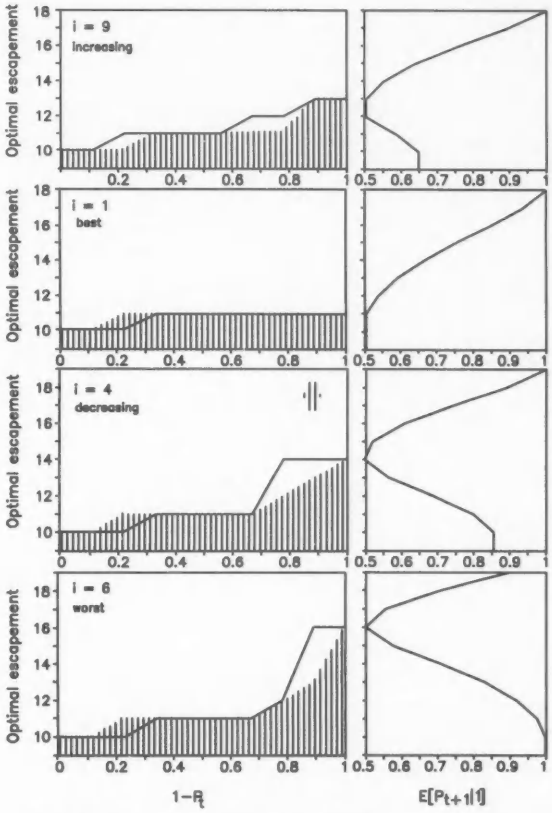

FIG. 7. Optimal controls for prototype III when a discount rate α = 0.95 is used. Other parameter values are as in Fig. 6.

alternative stock–recruitment curves intersect. For example, the least informative escapement level in Fig. 5 for $i = 9$, is 13; Bayes equivalent escapement targets for $1 - P_t$ close to 0.8 are thus very uninformative. The location of the gaps in escapement levels coincides precisely with the location of the uninformative regions. Deliberate experimentation away from the Bayes equivalent uniformative controls is optimal in those cases. When the optimal feedback responses are bang-bang, escapement targets may also depart from the Bayes equivalent optima, avoiding the uninformative region. We will use the term "probing" to refer to these departures between the actively adaptive and Bayes equivalent optimal escapement targets. Walters (1986) defined a probing action as "any change in management tactics that is deliberately intended to produce an informative response in the system state or outputs". Probing departures in the prototypes analyzed here may be worth undertaking towards both sides of the uninformative region; we will refer to these environmental actions as "upward probing" and "downward probing", when optimal escapement levels are respectively higher and lower than the Bayes equivalent ones. As we shall see later, Bayes equivalent controls may also be very informative, even though they are not prescribed on that basis. In general, actions that imply a departure from the historical policy are informative, although they do not necessarily involve a deliberate experimental shift or probing.

Consider first prototype I. Figure 5 shows that unless the probability $1 - P_t$ placed on the most conservative model is high (the actual P_t value depends on the environmental conditions) escapement goals approach the Bayes equivalent optima, and are closer to the optima for the more productive model 1. These levels are below the uninformative region. Active probing either upward or downward or both is favored only when the environmental-forcing hypothesis appears very likely, and then Bayes equivalent targets lean more towards the optima for model 2, falling within the uninformative region. This occurs at lower $1-P_t$ values during favorable environments due to the lower location of the uninformative region. Both policies, Bayes equivalent and actively adaptive, are overall not conservative. This is particularly striking during poor environmental conditions (such as $i = 6$), where a risk-averse prescription would be to behave according to the most pessimistic scenario. Curiously, under these poor conditions, the actively adaptive policy is slightly more cautious over most of the range of P_t values; upward shifts in the optimal escapements when $i = 4$ and $i = 6$ are not related to their information content since Bayes equivalent optima are well below the uninformative region. Rather, it appears that the optimal policy cautiously responds to anticipating that future observations might favor the more pessimistic model.

In prototype II, the contrast between the productivity levels implied by the alternative models is not as dramatic as in prototype I (results for prototype II are not shown here, but see Parma 1989 for details). Also, predictions of the alternative models are closer. As a result, the Bayes equivalent policy was overall less informative than in prototype I. Yet, the qualitative behavior of the computed policies are similar in both prototypes.

Results for prototype III differed from the previous in a number of ways. Bayes equivalent optima during favorable conditions (Fig. 6, $i = 9$ and $i = 1$) were uninformative for most values of P_t. Nevertheless, upward probing was favored only when the credibility of the environmental-forcing hypothesis was high and the risk of recruitment depression by density dependence was low; active and passive policies coincided otherwise. In contrast to the previous prototypes, upward probing would not result in an increase in recruitment if model 2 were true, since both models prescribe low escapements during favorable environments. The risk of recruitment depression due to overcompensation under model 1 also favored low escapement levels during poor environmental conditions. Unless recruitment failure by overharvesting during unfavorable conditions appeared very likely, the optimal decision was to practically ignore this risk and manage the stock according to the most productive model. The shift in Bayes equivalent targets towards levels approaching the optimal for the environmental-forcing hypothesis was rather abrupt and only occurred when the probability assigned to model 2 was close to 0.8. Upward probing was again favored over this range.

We see that in some cases actively adaptive escapement controls differ markedly from their Bayes equivalent counterparts. However, expected gains derived from deliberate experimentation were marginal. The value of Bayes equivalent policies computed over a 20-yr horizon was never below 98% of the corresponding value of actively adaptive policies. This was true for all three prototypes.

Summarizing, the results described so far indicate that probing either upward or downward may be favored when Bayes equivalent policies lead to uninformative decisions. Downward probing always results in escapement levels intermediate

between those optimal for models 1 and 2. Here probing is in the direction of "recognized yield opportunities," as was the case in the prototypes discussed by Walters (1981). Minor downward probing was favored especially during poor environmental conditions when the environmental-forcing hypothesis had high credibility. Upward probing at times implied forcing the stock to levels above those optimal for the more pessimistic model, which would entail some costs in yield even if model 2 proved correct; it was only favored when the credibility of the environmental-forcing hypothesis was very high.

Optimal policies were extremely sensitive to the choice of discount rate. When a value of $\alpha = 0.95$ was used (in place of $\alpha = 0.99$ as used when computing the policies in Fig. 5 and 6) upward probing was severely restricted. The effect was particularly marked in prototype III (Fig. 7). Bayes equivalent escapement targets for $i = 9$ and $i = 1$ are very similar to those in Fig. 6. However, although those levels are completely uninformative, the actively adaptive policy is practically indistinguishable from the passive policy. Also, escapement levels above the uninformative region were no longer optimal for $i = 6$, although downward probing was still favored. Results for the other prototypes are illustrated in Parma (1989). Apparently, with high discount rates, current catch losses incurred by raising the escapement levels were no longer overcome by the resulting learning benefits. The effects of changing the discount rate on the optimal policies are probably very marked in our prototypes because $l = 1$ was used in all trials. This implies that what is not harvested today can always be harvested tomorrow so, in the case of $\alpha = 0.99$, 99% of the year t catch losses incurred by upward probing can be recovered in year $t + 1$. As anticipated, gains in expected discounted yield resulting from following actively adaptive policies as compared with Bayes equivalent policies were again very small when using $\alpha = 0.95$ (the value of Bayes equivalent policies over a 20-yr horizon was never below 99% that of actively adaptive policies in any of the prototypes).

Optimal policies computed with $\sigma = 0.5$ exhibited the same qualitative patterns described above. The effect of increasing the process noise was in general to favor more drastic probing due to the larger width of the uninformative region.

Lags in Observing Population Responses

In order to explore the effects of increasing the lag coefficient k, a limited number of optimization trials were performed using $k = 1$. In that case, the optimal escapements depend not only on P_t and i_t, but also on the previous escapement level S_{t-1}. The analysis of these multi-dimensional feedback responses becomes very involved and the computed optimal policies are less comprehensible. Here we will not attempt to describe in detail the behavior of the policies computed for the different prototypes; rather, we will focus on the commonalities and main differences of these policies with the ones described for $k = 0$. Bayes equivalent escapement targets were very similar to those described for $k = 0$ throughout most of the range of S_{t-1} values. Their dependence on the previous escapement S_{t-1} was weak. Only a slight upward shift, especially during unfavorable environmental conditions, was produced in response to low S_{t-1} levels. This effect is qualitatively similar to that shown in Parma (1990) for the case of fully-observable dynamics: present escapements should be raised if future spawning targets are likely to be unfeasible. Aside from this, the policy was again to harvest the stock at rates close to those optimal under the density-dependence hypothesis unless a high credibility was given to the alternative model. As explained, these escapement levels are in general informative. Conflict between present yield and learning only arises when the environmental-forcing hypothesis appears very likely. Then, Bayes equivalent escapements shift towards those optimal for model 2, falling within the uninformative region.

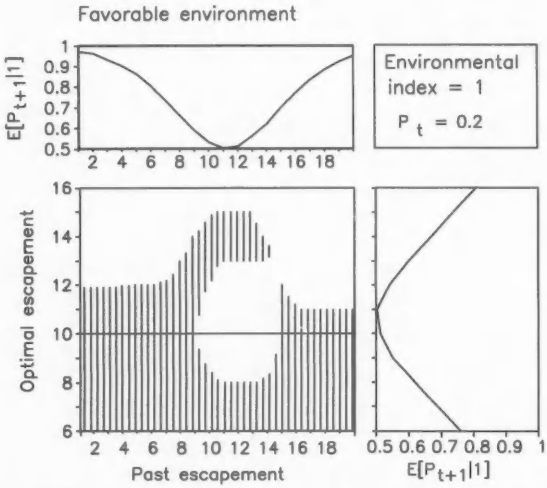

FIG. 8. Effect of past escapement levels S_{t-1} on optimal current decisions, when the environmental-forcing hypothesis is given high credibility, and the environmental conditions correspond to the most favorable in the 10-yr cycle. Results are for prototype I in Fig. 3 (with $\sigma = 0.3$; $k = 1$; $l = 1$ and $\alpha = 0.95$). Passive policies are bang-bang with escapement targets indicated by the solid line. Actively adaptive optimal escapements for each S_{t-1} value correspond to the maximum feasible level within the shaded region. Panels on the right show (on the x axes) a measure of the information content of the escapement levels on the y axes. $E[P_{t+1}|1]$ is the expected value of P_{t+1} when $P_t = 0.5$ and model 1 is true, for the range of escapement levels on the y axes. Values of $E[P_{t+1}|1]$ close to 0.5 indicate uninformative escapements. Top panels show the index for the information content of the previous harvest controls S_{t-1} on the x axes.

In contrast to Bayes equivalent controls, actively adaptive optima were strongly dependent on previous escapement levels and departures between active and passive policies were in general stronger here than with $k = 0$. The results corresponding to prototype I (with $\sigma = 0.3$ and $\alpha = 0.95$) will be used to illustrate the behavior of these policies. Fig. 8 and 9 show the dependence of optimal escapements on past management actions under different environmental conditions when a high probability is assigned to the environmental-forcing hypothesis ($P_t = 0.2$). As before, actively adaptive escapements correspond to the maximum feasible level within the shaded region; solid lines represent Bayes equivalent escapement targets. Controls are plotted as a function of the previous escapement level S_{t-1}. Panels on the right-hand side of the figures show the relative information content of the escapement levels on the y axes. Panels at the top show the relative information content of the previous escapement level S_{t-1} on the x axes. In both cases, the information content of an escapement level S is given as the expected value of P_{t+1} when $P_t = 0.5$ and model 1 is the true model, given that S is the escapement level at time $t - 1$.

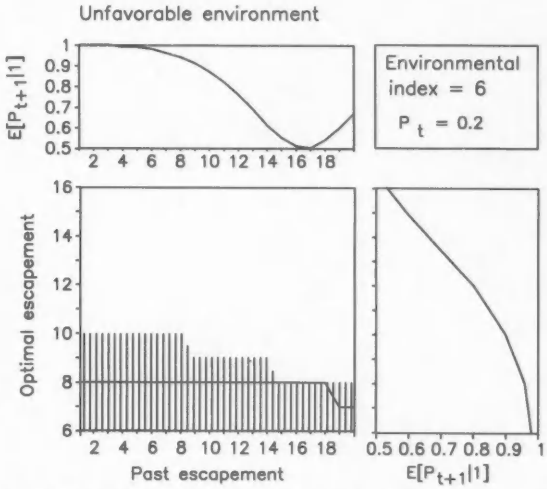

FIG. 9. Effect of past escapement levels S_{t-1} on optimal current decisions, when the environmental-forcing hypothesis is given high credibility, and the environmental conditions correspond to the least favorable year in the cycle. Results are for prototype I in Fig. 3 (with $\sigma = 0.3$; $k = 1$; $l = 1$ and $\alpha = 0.95$). Other details are as in Fig. 8.

Optimal escapements deviated in two ways from the Bayes equivalent ones: (a) probing outside the uninformative region and (b) cautious upwards shifting. As in the case of $k = 0$, major probing (either upward or downward) occurred during favorable environmental conditions (Fig. 8), when Bayes equivalent escapements were uninformative. The difference here is that probing only took place when the information content of the past management action was low ($E[P_{t+1}|1]$ close to 0.5). Away from these regions, actively adaptive controls tended to be in fact more cautious than the Bayes equivalent ones. Cautious upward shifts were more marked during poor conditions (Fig. 9). In this case, only when the past escapement level was uninformative did the optimal escapements coincide with the highly informative and nonconservative Bayes equivalent ones. At the other extreme (where $E[P_{t+1}|1]$ is close to one) the optimal control was intermediate between the Bayes equivalent and the optimal target for model 2, $S^* = 12$. Knowing when to probe is well determined, but the direction of probing is not clear. In Fig. 8 probing is first upward and then the direction flips at higher (although still uninformative) values of S_{t-1}. There is probably a marginal gain in probing upwards versus probing downward in this case. Indeed, only downward probing occurred when the environmental state corresponded to $i = 2$ instead of $i = 1$. In addition, the direction of probing was found to be sensitive to minor changes in the scale and grid extreme values used. This appears to be the case in all optimization trials done using $k = 1$. Cautious upward shifts were present in most situations; in particular, escapements tended to be higher the lower the value of S_{t-1}, especially when the environmental-forcing hypothesis was very likely. In spite of the noticeable differences between the Bayes equivalent and optimal policies, their value functions were again very close. In no case did differences exceed 1%.

The qualitative behavior of optimal policies and their response to the additional state variable S_{t-1} can be interpreted in very simple terms: if there is a delay in detecting the population response to past experimental actions, then it is better to be cautious and allow higher escapement levels to hedge against the possibility that results from those past probing actions favor the more pessimistic model. It is particularly important to be cautious when past spawning levels were simultaneously informative and low, this is, when downward probing took place in the past. If, on the other hand, past management actions were uninformative, probing may be worthwhile or not depending on whether the Bayes equivalent policies fall within or outside the uninformative region. In other words, when, given the value S_{t-1}, the information state P_{t+1} will remain approximately at its current value whichever the outcome R_{t+1}, the optimal policy is similar to that evaluated for $k = 0$. The effect of past escapement levels is then two-fold: (1) low past escapement levels may put at risk the feasibility of future optimal spawning targets, and (2) they affect the dynamics of the information state and thus influence future optimal targets.

TABLE 1. Performance of constant harvest rate (CHR) and optimal risk-averse (RA) policies for the two-hypotheses optimization problem of prototypes in Fig. 3. H^* is a quasi-optimal exploitation fraction when the stock size is approximately equal to the "historical" mean (N_t = 16). The value of any given policy is given as the expected discounted yield over a 20-yr horizon, expressed as a percentage of the maximum expected discounted yield. Maximum and minimum policy values over the range of initial environmental conditions are given for each level of credibility when initial stock size is equal to the historical mean value. Parameter values are $k=0$, $l=1$, $w=10$, $\sigma=0.3$ and $\alpha=0.95$.

		Credibility of model 1				
		0	0.2	0.5	0.8	1
Prototype I	H^* =	0.17	0.20	0.45	0.45	0.47
	CHR value =	97–99	85–91	84–89	92–94	98
	RA value =	97–99	96–99	96–97	97–98	98
Prototype II	H^* =	0.17	0.20	0.23	0.37	0.37
	CHR value =	97–99	90–97	86–90	92–95	98
	RA value =	97–99	96–99	96–98	97–89	99
Prototype III	H^* =	0.11	0.13	0.15	0.22	0.23
	CHR value =	85–91	81–87	78–85	88–90	93
	RA value =	81–87	84–88	88–90	91–92	93

Constant Harvest Rate Policies

The performance of constant harvest rate policies compared with optimal policies was in general good when there was perfect information and the population level was around the "historical" mean value (Table 1). This was particularly so for prototype II. When the two models appeared equally likely, however, performance of constant harvest rate policies degraded substantially. Expected discounted yields over 20 yr were in some cases considerably below optimal yield (reductions of up to 22% were computed for our prototypes). The poor performance of constant harvest rate policies when uncertainty is high must be due to their nonadaptive nature. The value of constant harvest rate policies was computed by actually fixing the harvest rate throughout the length of the management horizon. Future observations, although they might be highly informative, did not feed back into the system. In other words, passive learning was not allowed in the computations.

Risk-Averse Policies

Optimal risk-averse policies for the two-hypotheses problem differed markedly from risk-neutral policies: while risk-neutral

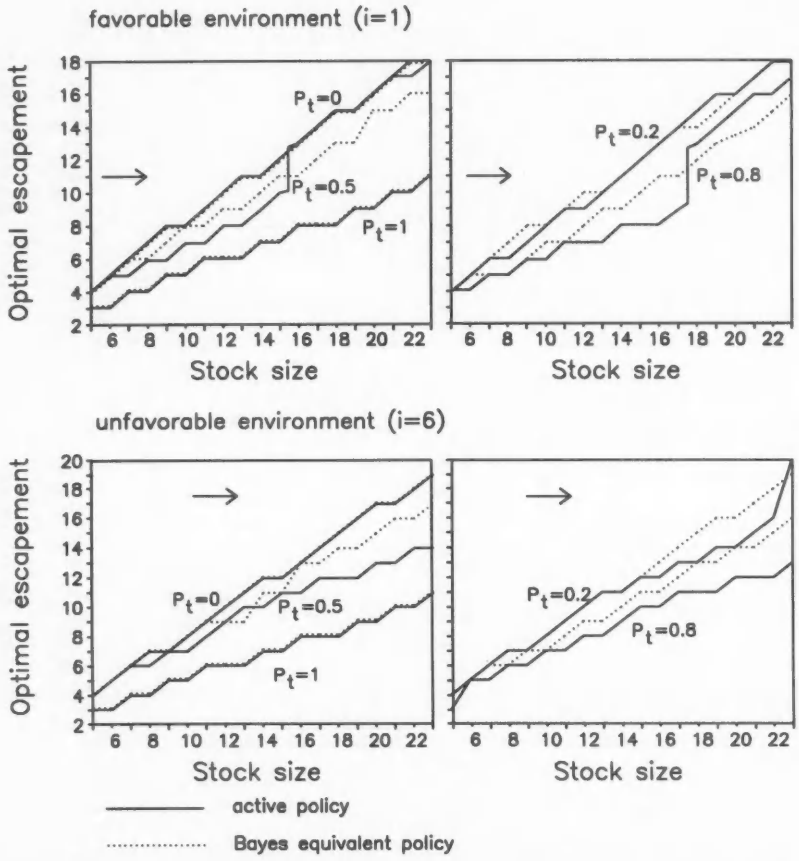

FIG. 10. Probing departures between active and passive optimal risk-averse policies. Curves correspond to different levels of P_t, the credibility of the density-dependence hypothesis. Panels on the left show optimal controls for $P_t = 0$ (top line), $P_t = 0.5$ (intermediate lines), and $P_t = 1$ (bottom line). Panels on the right show controls for $P_t = 0.2$ (top two lines) and $P_t = 0.8$ (bottom two lines). Arrows mark the escapement levels that are completely uniformative. Results are for prototype I in Fig. 3 (with $\sigma = 0.3$, $l = 1$, $k = 0$, and $\alpha = 0.95$).

policies are in general bang-bang, optimal risk-averse escapements tend to increase approximately linearly with population abundance. Figure 10 illustrates the behavior of the optimal risk-averse policies computed for prototype I. Optimal escapements are plotted as a function of stock size for extreme environmental conditions and various P_t levels. Actively adaptive escapements are illustrated together with their Bayes equivalent counterparts. The linear dependency of the optimal escapements on the stock size was more marked for Bayes equivalent policies (dashed lines) than for the actively adaptive policies (solid lines). The behavior of Bayes equivalent policies contrasted with that of risk-neutral passive policies, where escapements at intermediate P_t levels were biased towards the more optimistic model. Here, instead, when the alternative models had equal credibility ($P_t = 0.5$, left panels), Bayes equivalent controls were very cautious and approached those optimal under the more pessimistic model (i.e. those for $P_t = 0$).

The question of interest here is how the optimal policy responds to variations in the credibility of the alternative models and, in particular, whether or not the use of a risk-averse utility restrains the occurrence of probing for information. The comparison of the actively adaptive and Bayes equivalent risk-averse optimal policies, computed for the three prototypes using a discount rate of $\alpha = 0.95$, indicated that probing was still worthwhile under some system states. Figure 10 shows some departures between active and passive controls, which always correspond to experimental shifts away from the uninformative region. The arrow in each panel signals the escapement level that is completely uninformative (i.e. at the center of the uninformative region where $P_{t+1} = P_t$). The direction of probing was consistently upward when Bayes equivalent escapements were above the least informative level and downward otherwise. Notice that the lines corresponding to Bayes equivalent and actively adaptive controls cross at the level indicated by the arrow. As a result, probing was predominantly downward (higher overall harvest rates) during poor environments, and in both directions during favorable conditions. Probing upward only occurred when the stock size was large so that an inform-

ative spawning level could be reached while maintaining medium catch levels. Notice for example the absence of upward probing for $P_t = 0.2$ and $i = 1$ even though the Bayes equivalent escapement is right at the level indicated by the arrow. Downward probing during favorable conditions (which implies low escapement levels, since the uninformative region is low) was restricted when the environmental-forcing hypothesis was very likely ($P_t < 0.3$). The same overall pattern was exhibited by the optimal policies computed for the other prototypes, although probing shifts were in general weaker.

Gains in expected discounted yield over 20 yr computed for actively adaptive risk-averse policies as compared with Bayes equivalent risk-averse policies were again small (up to 5% in prototype I, 4% in prototype II, and 2% in prototype III). Performance of the optimal risk-averse policy in terms of expected discounted yield was close to that of the optimal risk-neutral policy in prototypes I and II, and less so in prototype III (Table 1). In the first prototypes, losses in expected discounted yield over a 20-yr horizon associated with the optimal risk-averse policies rarely exceeded 5% of the maximum value corresponding to risk-neutral policies. They outperformed the constant harvest rate policies for both prototypes I and II. The risk-averse policy performed poorly for prototype III, in some cases even worse than the constant harvest rate policy, which shows that risk aversion can in some cases demand a high penalty in terms of total catch.

Harvesting Strategies and Learning Rates

The effect that the different harvesting strategies have on the overall learning rates depends on the initial system states. Suppose for example that model 2, the environmental-forcing hypothesis, of prototype II were the true model and the population followed a deterministic trajectory with recruitment given by $F^2(S_t|i_t)$. Figure 11a shows for different harvesting strategies how the probability assigned to the true model would be updated as new data became available, if $\sigma = 0.5$ were used in that update, and the alternative models were initially assigned equal probabilities. The first recruitment observation in the trajectories there corresponds to an environmental index $i = 2$. Trajectories generated with active and passive risk-neutral policies are almost identical, which is consistent with the equivalence of their respective value functions. Constant harvest rate policies, on the other hand, led to very different trajectories depending on the harvest rate H. A harvest rate of 0.15 could be considered cautious, since it is intermediate between the optimal harvest rates for the stock–recruitment functions corresponding to the most and least favorable environments in model 2. Overall this is the least informative policy. Shifts in P_{t+1} under this harvest rate occurred only after the stock size increased beyond the uninformative region. With $H = 0.20$ and $H = 0.25$, informative states corresponded instead to escapement levels below the uninformative region. Trajectories generated under optimal risk-averse policies (not included in the figure) were intermediate between those generated with $H = 0.20$ and $H = 0.25$.

A contrasting picture was obtained when model 1 was chosen as the true model but it was assigned a very low initial credibility (Fig. 11b). The environmental index corresponding to the first recruitment observation was set to $i = 4$, so that the first series of observations corresponded to poor environments according to the false model. Under these conditions actively adaptive and Bayes equivalent risk-neutral controls diverged appreciably. As a result, learning rates were drastically

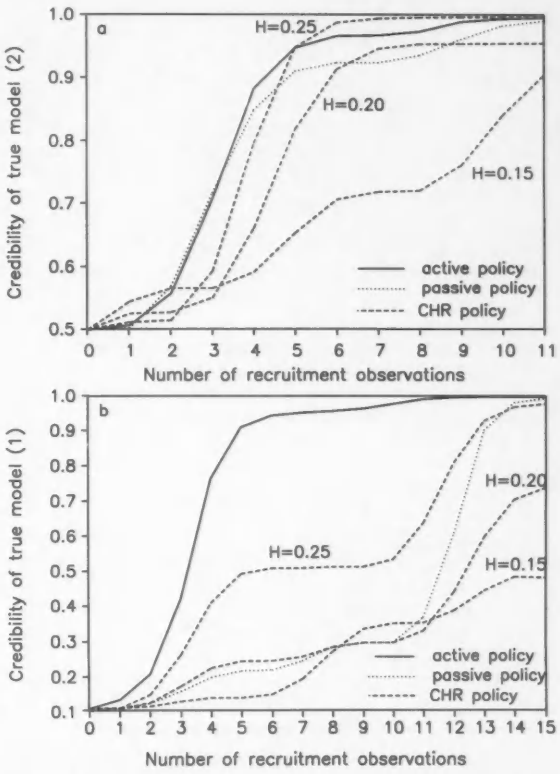

FIG. 11. Credibility of true model after x recruitment observations, under alternative harvesting regimes. Stock trajectory is deterministic; recruitment equals the median of the distribution predicted by the true model. Constant harvest rate policies have exploitation fractions given by H. Parameter values correspond to prototype II in Fig. 3 with $\sigma = 0.5$, $l = 1$, and $\alpha = 0.99$. (a) Model 2 is true and both models are initially assigned equal probabilities; environmental index for first recruitment observation is $i = 2$ ($i = 1$ is the most favorable environment and $i = 6$ the least). (b) Model 1 is true and has low initial credibility; environmental index for first recruitment observation is $i = 4$. Notice the different scale on the x axes.

increased by active experimentation as compared with passive learning. Probing in both directions took place over the deterministic trajectory and major shifts in the credibility of the true model occurred following downward probing during the worst environmental conditions. A similar contrast between active and passive trajectories was obtained when model 2 was chosen as the true model. For constant harvest rate policies, low harvest rates were again less informative than high ones. Initial stock size was high and so even high harvest rates were not sufficient to lower the escapement levels below the uninformative region during the period of unfavorable environmental conditions. The same was true for the optimal risk-averse policy, which produced a trajectory similar to that of $H = 0.2$.

The extent to which the deterministic trajectories in Fig. 11 depart from mean trajectories, as could be generated with Monte Carlo simulations, is difficult to judge. The values of R_{t+1} on the nominal path in the figures correspond in each time step to the median of the actual random R_{t+1} values. Hence, since P_{t+1}

is monotonic on R_{t+1}, single-step updates result in the median of the random P_{t+1} values. Distortion may be larger in the case of constant harvest rate policies since "natural experiments" (departures of the escapement levels from their nominal trajectory caused by random realizations of Z) are also removed. Scenarios similar to those described by Walters (1984a), where the system can be temporarily trapped into uninformative states, can also be visualized here, although the picture is complicated by the cyclic shift of the uninformative region.

In spite of these limitations, the analysis indicates that experimental actions may accelerate the learning process considerably whenever passive policies result in uninformative decisions. The effect of any given harvesting strategy upon learning rates depends on the actual sequence of spawning levels allowed. In constant harvest rate and risk-averse policies, optimal escapements are largely a function of stock size; the learning rates associated with those policies therefore vary depending on the size of the stock at the beginning of the management horizon.

Conclusions and Discussion

Results indicate that optimal passive policies may perform nearly as well as actively adaptive policies, even though deliberate experimentation with escapement levels is usually favored when passive policies lead to uninformative system states. This is an advantage since Bayes equivalent policies are easier to compute. They can be used as baseline policies in analyses of optimal harvesting strategies in more complex situations. When the objective is to maximize future yield, optimal passive escapements are overall nonconservative and highly informative. Only when the odds of the environmental-forcing hypothesis are very high do Bayes equivalent escapements approach the higher, uninformative levels which are optimal under that hypothesis. Probing away from the range of spawning levels for which alternative models make consistent predictions is then favored. The direction of probing is predominantly upward (higher escapement, lower catch) during favorable environments and downward during poor ones. When unfavorable conditions are anticipated and both models are equally likely, prescriptions of both active and passive policies coincide: low, informative escapement levels should be allowed. Lowering spawning levels below their historical average (over poor environments) when unfavorable conditions are expected not only is the best experiment in terms of hypotheses testing, but it is also the best decision based on weighing alternative population responses (models) according to their respective credibility, even if future learning is neglected in the analysis. Behaving as if the more pessimistic model were the true one, when in fact the two appear equally likely, may result in considerable yield losses (up to 28% over 20 yr in our prototypes). Cautious policies under which density-dependent and environmental effects cannot be discriminated should be avoided if the goal is to maximize total expected yield.

When a risk-averse management objective is pursued, optimal passive escapements tend to increase linearly with population abundance. Thus, there is always some range of population sizes for which optimal escapements are uninformative, this is, they fall in the range of spawning levels for which alternative models predict similar population responses. Probing either above or below that range may be favored in those cases. The use of a risk-averse objective function restrained probing upward whenever raising the escapement levels would imply severe catch reductions. Probing downward was also limited when the odds placed on the more conservative model were high. However, minor downward probing was still favored under poor environmental conditions.

When the two models had equal credibility, optimal risk-averse escapements were on average closer to those optimal under the environmental-forcing hypothesis. This is contrary to the behavior of risk-neutral controls which favored the less conservative, and more productive, model 1. Optimal risk-averse escapements during unfavorable conditions were intermediate between those optimal under the alternative models; during favorable conditions they were close to the optima for the environmental-forcing hypotheses.

The performance of optimal risk-averse policies was close to that of the optimal risk-neutral policies, with the exception of prototype III, while that of nonadaptive constant harvest rate policies was poorer when P_t was close to 0.5.

The results of this study may lead one to conclude that passive policies are in general just as good as active ones. On the other hand, in contrast to the present work, Ludwig and Hilborn (1983) tested active versus passive strategies by simulation, and found substantial difference in performance. Two simplifying assumptions made in our analysis are worth considering before drawing any general conclusion: first, measurement errors are neglected and, second, the alternative hypotheses are cast into two specific SRR's. We discuss each of these in turn.

Since measurement errors are neglected, the informative content of an experimental outcome is overestimated. This can favor probing. At the same time, the informative value of other policies (the Bayes equivalent among them) is also exaggerated and, therefore, strong probing may not be worthwhile. Basically any policy may be sufficiently informative.

The alternative models are treated as simple hypotheses. When competing hypotheses of the type dealt with here are postulated in reality, the alternatives appeal to qualitatively different mechanisms regulating population size rather than to different specific stock–recruitment functions. As such, each hypothesis would be more realistically represented as a family of SRR's, within which parameter values are allowed some degree of flexibility (a problem that would be untractable with the setting used here). In that situation, a recruitment observation might lead to rejection of some particular stock–recruitment function, while its underlying mechanistic hypotheses might not be falsified. Consider for example the optimal controls in Fig. 6 for the poorest environmental conditions (i = 6). Drastic probing in the direction of allowing high escapement levels (in fact the highest permitted in the optimization trial) is favored when model 2 appears very likely. Allowing large spawning abundances when a poor environment is anticipated is informative only in the context of the specific SRR's chosen to represent the alternative hypotheses: the two functions generate quite distinctive predictions under these conditions (see Fig. 3). If, instead, the alternative hypotheses were stated qualitatively, they would both coincide in predicting poor recruitment levels. If the experiment resulted in very low recruitment, although that outcome would be very unlikely under the specific SRR in model 2, it would still be consistent with the environmental-forcing hypothesis. Likewise, the value of probing downward during favorable conditions can be dismissed with a similar argument. The effect of treating the alternative hypotheses as simple instead of composite hypotheses is then to exaggerate the learning speed of the decision maker and to occasionally favor "probing in the wrong direction". In addi-

tion, it may avoid the parameter estimation traps which Ludwig and Hilborn (1983) observed with the passive strategy. Increasing the process noise (the value of σ) in order to counteract some of the problems, although it may reduce the learning speed, also has the undesirable effect of underestimating the importance of learning. This is because expected yield from any given model can become less sensitive to departures of the implemented policy from the optimal.

The assumption that P_{t+1} is solely a function of P_t, R_{t+1}, S_{t-k}, and i_{t-k} excludes the possibility that ancillary information favoring one or the other hypothesis affects the credibility of the alternative models. This can be a problem here, mainly due to the nature of the alternative models. Discriminating between qualitatively different mechanisms controlling the dynamics of the population may involve more than a purely statistical criterion (i.e. the differential fitting of the alternative models, in this case).

Decision makers exhibit more complex behavior than the simple objective one assumed in our analysis. On the one hand, probabilities placed on the alternative hypotheses are usually not mechanically updated (as Bayes theorem predicts) when new data become available (see Walters 1986 for a discussion). Also, management prescriptions derived objectively for some given P_t may not always be implemented. Strong risk aversion causes pendular shifts in the credibility of the alternative models in response to the anticipated changes in mean productivity of the stock, predicted by the environmental-forcing hypothesis. The possibility that fluctuations are driven by an extrinsic cycle appears more likely when the period of low productivity is approaching. This reflects a reluctance to use low escapement levels during those years, which would be the optimal decision if the two models were equally credible. Also, the detection of a decline in population abundance prompts the implementation of conservative regulation even though evidence of overfishing may be missing. Faith that favorable periods will return and the population will naturally recover usually becomes faint under those circumstances.

The Pacific halibut can be used to illustrate these problems. Variation in the historical series of halibut year-class abundance has been linked to a number of environmental variables presumably affecting larval transport processes (Parker 1989). However, no biologically plausible mechanism has yet been identified in support of the hypothesis of cyclic environmental forcing, so as to substantiate a prediction that recruitment rates will continue to cycle in the future. Strong risk aversion and the remarkable fit of the recruitment trend with a sinusoidal function (Fig. 1) rescue that hypothesis, especially during the unfavorable years of the postulated environmental cycle. Risk-averse behavior of the type described may have the undesirable effect of indefinitely propagating the cycles of boom and bust in the fishery. The catch-quota recommendations made by the scientific staff of the International Pacific Halibut Commission are currently based on a constant harvest rate: the current exploitation fraction is intermediate between the harvest rates that are optimal under the alternative recruitment models. Our results indicate that, when the uncertainty level is high, constant harvest rate policies may perform poorly. This is due to the nonadaptive nature of the policies explored in our analyses. Mixed strategies, in which harvest rates are held constant for a given period (say 5 yr) following which the harvest level is corrected according to the new information gathered should be considered for the Pacific halibut. Policies of this type are suitable for analysis with Monte Carlo simulations when models of higher complexity are desirable to represent the dynamics of real-case populations.

The ability to discriminate between the alternative hypotheses may be greatly improved by implementing passive optimal policies, which result from weighing possible population responses according to a priori probabilities assigned to the alternative models. Maintaining relatively low stock levels when unfavorable conditions are expected may prove very difficult to implement even when those levels correspond to the optimal passive decision (derived with no account for the effect of harvest controls on future learning). Burkenroad (1951) proposed that fishery regulations should be designed as controlled experiments. In our results, informative management actions did not necessarily involve true probing shifts away from optimal passive escapement levels. However, they may still be considered "experiments" in a broader sense: optimal policies, whether passive or active, involved a departure from the historical course of action, such that the system was forced to a state under which the alternative hypotheses predicted different population responses.

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Appendix A. Proof of Equivalence Between Alternative Dynamic Programming Formulations of the Two-Hypotheses Optimization Problem

Here we show that the dynamic programming formulation of the two-hypotheses problem, involving the computation of two separate value functions (one for each model) combined as in equation (4) at each single-period maximization, is equivalent to the formulation in equation (5), when the level of credibility assigned to each model is updated by means of Bayes theorem. More generally, under any given feedback control law π_t, where each control S_t^* depends on (R_t, S_{t-1}, P_t, i_t), if P_{t+1} is as given by equation (3), the function

$$J_t^*(R_t, S_{t-1}, P_t, i_t) = P_t J_t^1(R_t, S_{t-1}, P_t, i_t) + (1 - P_t) J_t^2(R_t, S_{t-1}, P_t, i_t)$$

where

$$\text{(A.1)}\quad J_t^1(R_t, S_{t-1}, P_t, i_t) = U(N_t - S_t^*) + \alpha E[J_{t+1}^1(F^1(S_{t-k})e^{\sigma Z}, S_t^*, P_{t+1}, i_{t+1})]$$

$$J_t^2(R_t, S_{t-1}, P_t, i_t) = U(N_t - S_t^*) + \alpha E[J_{t+1}^2(F^2(S_{t-k}|i_{t-k})e^{\sigma Z}, S_t^*, P_{t+1}, i_{t+1})]$$

for $N_t = R_t + lS_{t-1}$, is equivalent to

$$\text{(A.2)}\quad J_t^{**}(R_t, S_{t-1}, P_t, i_t) = U(N_t - S_t^*) + \alpha E[J_{t+1}^{**}(R_{t+1}, S_t^*, P_{t+1}, i_{t+1})],$$

where the expectation on the right-hand side is now taken across the two alternative stock–recruitment models. As a corollary, actively adaptive optimal controls can be searched for by directly maximizing equation (A.2), which is an equivalent formulation of equation (5) in the text.

Proof

We will use induction to show that

$$J_t^{**}(R_t, S_{t-1}, P_t, i_t) = P_t J_t^1(R_t, S_{t-1}, P_t, i_t) + (1 - P_t) J_t^2(R_t, S_{t-1}, P_t, i_t) = J_t^*(R_t, S_{t-1}, P_t, i_t).$$

Suppose that $J_{t+1}^{**}(R_{t+1}, S_t, P_{t+1}, i_{t+1})$ satisfies the induction hypothesis and rewrite equation (A.2) as

$$\text{(A.4)}\quad J_t^{**}(R_t, S_{t-1}, P_t, i_t) = U(N_t - S_t^*) + \alpha \int_0^\infty [P_{t+1} J_{t+1}^1(R_{t+1}, S_t^*, P_{t+1}, i_{t+1}) + (1 - P_{t+1}) J_{t+1}^2(R_{t+1}, S_t^*, P_{t+1}, i_{t+1})] p(R_{t+1}) dR_{t+1},$$

where $p(R_{t+1}) = P_t p(R_{t+1}/1) + (1 - P_t) p(R_{t+1}/2)$ is the pdf of R_{t+1}, which is of course conditional on S_{t-k} and i_{t-k}. From equation (3) we have that

$$P_{t+1} = \frac{P_t p(R_{t+1}|1)}{p(R_{t+1})}$$

and, by algebra with the pdf of R_{t+1},

$$(1 - P_{t+1}) = \frac{(1 - P_t) p(R_{t+1}|2)}{p(R_{t+1})}$$

Substituting both equations into (A.4) yields

$$J_t^{**}(R_t, S_{t-1}, P_t, i_t) = U(N_t - S_t^*) + \alpha \left[P_t \int_0^\infty J_{t+1}^1(R_{t+1}, S_t^*, P_{t+1}, i_{t+1})\, p(R_{t+1}|1) dR_{t+1} + (1 - P_t) \int_0^\infty J_{t+1}^2(R_{t+1}, S_t^*, P_{t+1}, i_{t+1})\, p(R_{t+1}|2) dR_{t+1} \right]$$

Equation (A.3) follows directly after substituting the recursive equations (A.1). Since the initial value function in the backwards recursion $J_T^{**}(R_T, S_{T-1}, P_T, i_T) = U(N_T)$ satisfies the induction hypothesis, (A.3) holds for any t.

Ranking Loci for Genetic Stock Identification by Curvature Methods

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Measures of the utility of loci in genetic stock identification problems are usually not based on the method of maximum likelihood, which is the actual statistical procedure used to estimate stock contributions. We present a general procedure, derived from the likelihood method, for assessing the utility of baseline data. The method depends on the curvatures of potential likelihood surfaces and can be used prior to mixture sampling. We also develop a real time implementation of a curvature measure and apply it to simulated mixture samples. The error in likelihood estimation depends on the amount of variation in genotype frequencies between reference samples as well as the location of the center of that variation. The curvature measure accounts appropriately for both factors and, in addition, is able to quantify the synergistic interaction of multiple loci. The curvature approach and simulation results are also applied to the problem of sampling allocation.

Les mesures portant sur l'utilité des loci dans la résolution des problèmes d'identification des stocks génétiques, ne reposent habituellement pas sur la méthode du maximum de vraisemblance, qui est la méthode statistique utilisée pour évaluer les contributions des stocks. Nous proposons une méthodologie générale, dérivée de la méthode du maximum de vraisemblance, afin d'évaluer l'utilité des données de référence. La méthode dépend de la courbure des surfaces de vraisemblance possibles et peut être appliquée avant l'échantillonnage des mélanges. Nous avons aussi développé une mise en application en temps réel de la mesure de la courbure, et nous l'appliquons à des échantillons de mélanges simulés. L'erreur associée à l'évaluation de la vraisemblance dépend de l'importance de la variation des fréquences génotypiques entre les échantillons de référence ainsi que de la position de ce centre de variation. La mesure de la courbure permet d'expliquer adéquatement les deux facteurs et, en outre, permet aussi la quantification des interactions synergiques des loci multiples. L'approche par les courbures et les résultats des simulations sont aussi appliqués au problème de l'allocation des échantillons.

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Genetic stock identification (GSI) utilizes genetic differences among individual fish stocks (the baseline samples) to determine the composition of mixtures of fish from those stocks (Milner et al. 1981; Millar 1987). The basic data are the allele frequencies at each genetic locus in the baseline samples and the mixture sample. Typically, several to many loci (and sometimes other data types) are included in the analysis (Fournier et al. 1984; Milner et al. 1981; Wood et al. 1989). The quantities estimated are the proportions that each stock contributes to the mixture. GSI is thus a technique for which assessment of data quality is essential if the method is to succeed in mixed stock fishery management.

In this paper, we present a method that can be used to assess the quality of data for GSI. We concentrate on genetic (i.e. allele frequency) data, but the method can be applied to situations in which multiple data types are used (cf. Fournier et al. 1984; Millar 1987; Wood et al. 1989).

Each locus sampled in the baseline samples and the mixture sample contributes new information to the estimation procedure. However this information is obtained at a cost, both operational and computational. It is therefore important to assess the improvement in precision and accuracy of the estimate obtained by adding the information at each locus. We call the improvement in estimation precision and accuracy obtained by adding a set of loci the "utility" of that set.

Methods of evaluating the utility of loci, such as Nei's genetic distance (Nei 1972), the G statistic (Sokal and Rohlf 1981), allele frequency differences (Wood et al. 1987), and chi-square tests are ad hoc with respect to GSI and the likelihood method in that they do not use the same model as the GSI method, but intuitively appealing because gene frequency distributions are used. The difficulty with constructing a measure of locus utility based on maximum likelihood is that, unlike the preceding methods, likelihood methods generally depend on the mixture sample obtained. In the next section, we present a measure of locus utility that is based on the likelihood method, yet independent of mixture samples. This measure evaluates curvatures of potential likelihood surfaces that are generated by data at a specific locus (or group of loci), and we refer to it as a "curvature measure."

Theory and General Procedure

Statistical Model and Parameter Estimation

Consider a fishery with S stocks. (Table 1 contains a summary of definitions used in this section.) There are G

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TABLE 1. Summary of notation used in the text.

(1-i)	G	Number of genotypes;
(1-ii)	S	Number of stocks;
(1-iii)	$\theta = (\theta_1,\ldots,\theta_S)$	Vector of stock mixture proportions; $0 \le \theta_s \le 1$; $\sum_{s=1}^{S} \theta_s = 1$;
(1-iv)	$\hat{\theta} = (\hat{\theta}_1,\ldots,\hat{\theta}_S)$	MLE of stock mixture proportions; $0 \le \hat{\theta}_s \le 1$; $\sum_{s=1}^{S} \hat{\theta}_s = 1$;
(1-v)	$\Theta = (\Theta_1,\ldots,\Theta_S)$	Underlying stock mixture proportions; $0 \le \Theta_s \le 1$; $\sum_{s=1}^{S} \Theta_s = 1$;
(1-vi)	x_{gs}	Baseline frequency data: frequency of genotype g within stock s;
(1-vii)	$\mathbf{X}$	G by S matrix of baseline frequencies x_{gs};
(1-iix)	N	Size of mixture sample;
(1-ix)	$\mathbf{y}$	Vector of mixture sample genotypes $\left(\mathbf{y} \in \mathbb{N}^G \text{ and } \sum_{g=1}^{G} y_g = N\right)$;
(1-x)	$\mathcal{L}(\theta)$	Log-likelihood function $\sum_{g=1}^{G} y_g \left[\ln \sum_{s=1}^{S} x_{gs}\theta_s\right]$.

genotypes that any particular fish can have and the relative frequency of genotype g within stock population s is x_{gs}. We assume these baseline data are known exactly and denote the G by S matrix of baseline data by $\mathbf{X}$. Baseline data may be derived from gene frequencies at either a single locus or several loci. Our objective is to evaluate the utility of a set of baseline data for stock proportion estimation using GSI.

In the ocean, S stocks mix according to unknown proportions $\Theta = (\Theta_1,\ldots,\Theta_S)$; the objective of GSI is to determine an estimate for these proportions, which we simply call the mixing proportions. To do this, N fish are sampled at random from this mixture and the number of each of the G genotypes observed is recorded in the vector $\mathbf{y} = (y_1,\ldots,y_G)$. Since G is typically quite large, there will be many y_g that are 0. The probability distribution of the observed genotypes $\mathbf{y}$ is then multinomial with parameters N and

$$\left\{\sum_{s=1}^{S} x_{gs}\Theta_s\right\},\ g = 1, \ldots, G \text{ (e.g. Millar 1987).}$$

In GSI, the method of maximum likelihood (Edwards 1972) is used to estimate the unknown Θ and yields an estimate $\hat{\theta}$, the point at which the log-likelihood function $\mathcal{L}(\theta)$ is maximized. The likelihood function for this fishery model is given in Table 1. For a given mixed ocean sample $\mathbf{y}$ and set of baseline frequencies $\mathbf{X}$, there will be one value of stock proportions that maximizes the likelihood (subject to certain spanning conditions; Millar 1987); this is the maximum likelihood estimate (MLE) and is denoted by $\hat{\theta}(\mathbf{y}, \mathbf{X})$. Also note that we use a conditional maximum likelihood method which assumes that the baseline frequency distributions are known exactly.

Curvature of a Likelihood Surface and the Quality of an MLE

We choose to work exclusively with the log-likelihood rather than likelihood itself. Edwards (1972) provides a good introduction. For conceptual purposes, it is useful to think of $\mathcal{L}$ as a surface parameterized by the mixing proportions θ (see Fig. 1). With three stocks, $\mathcal{L}(\theta)$ is at its highest point above $\hat{\theta}$. In more dimensions $\mathcal{L}(\hat{\theta})$ represents an analogous "hyper-peak" of the hypersurface $\mathcal{L}$. Intuitively, a good MLE is one that has significantly more likelihood, with respect to the likelihood surface $\mathcal{L}(\theta)$, than other points nearby (Edwards 1972). That is, good estimates correspond to sharp peaks, less desirable estimates to flat peaks; Fig. 1 illustrates the concept.

The sharpness of a peak is measured by its curvature, which generalizes the second derivative of a function of one variable to functions of many variables. The curvature of the likelihood surface $\mathcal{L}$ at $\hat{\theta}$, measured in a particular direction, indicates how sharp the drop-off from $\mathcal{L}(\hat{\theta})$ is in that direction (see Fig. 2). Since the curvature is generally different in different directions, criteria must be used to choose which direction, or combination, is most indicative of the sharpness of the peak and thus the reliability of the estimate. These criteria will change according to the question that one wants to answer.

We choose a conservative criterion for our application: the curvature is computed in the direction of flattest descent from the surface peak. We choose a conservative measure since management use of GSI may typically require an accurate picture of all stocks affected by the fishery. The use of a conservative criterion also provides a "worst case" assessment of the utility of data in GSI, rather than an overly optimistic assessment. The resulting curvature measure, which we denote by $\zeta(\mathbf{y}|\mathbf{X})$, then indicates the magnitude of the worst case direction for the likelihood surface. This is "worst case" in the sense that points far from the MLE may still have considerable likelihood. Figure 2 demonstrates this point for two-dimensional surfaces. Just as there is one likelihood surface $\mathcal{L}$ and one MLE $\hat{\theta}$ for given baseline and mixture data (Berger and Wolpert 1984; Edwards 1972), there is one value of $\zeta(\mathbf{y}|\mathbf{X})$ for a given data set. In the Implementation Practicalities section, we show how to compute the curvature in the direction of flattest descent. Note, however, that at this point the criterion depends on the ocean mixture sample $\mathbf{y}$; this is not desirable so we first consider ways to remove that dependence.

Independence from Mixture Sample

Our goal is to find a measure of baseline data quality that is independent of the mixed ocean fishery sampling. That is, we want an indicator of the performance of maximum likelihood estimation in general, rather than for a particular mixture sample. The likelihood function $\mathcal{L}$ described above also depends

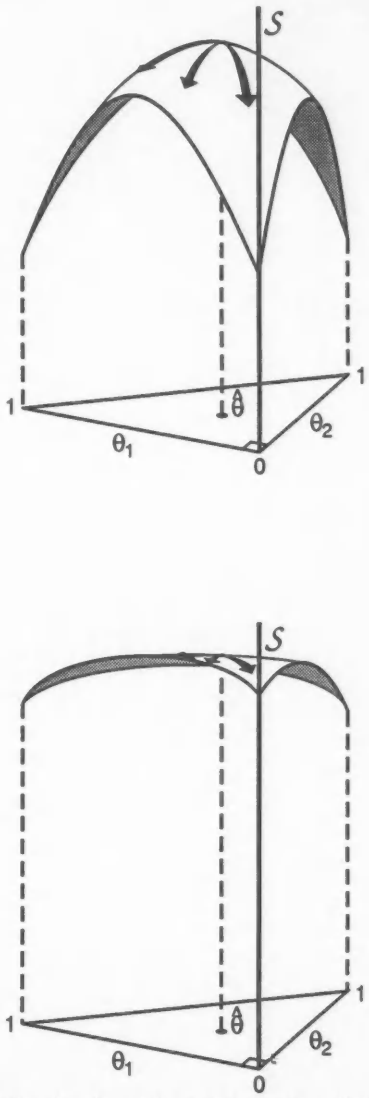

FIG. 1. Likelihood surfaces, $\mathcal{S}$, and their maximum likelihood estimates, $\hat{\theta}$, for two different data sets. The maximum likelihood, $\mathcal{S}(\hat{\theta})$, is the same in each case however, the upper surface represents the case of a relatively well supported and desirable estimation scenario. The lower illustration corresponds to the likelihood surface of a weaker estimate.

on the mixed ocean sample **y** and baseline data (see expression 1-x in Table 1). More explicitly, the likelihood function, for a given set of baseline frequencies **X**, should be denoted by $\mathcal{S}(\theta;\mathbf{y}|\mathbf{X})$ since it represents a family of functions of θ indexed by the multidimensional parameters **y**. The vector **y** also contains all of the information obtained from the mixed ocean sample. Thus, the parameterization of $\mathcal{S}$ by **y** translates into dependence of the MLE $\hat{\theta}$ and curvature measure ζ on the mixed ocean sample. The latter we sometimes write as $\zeta(\mathbf{y}|\mathbf{X})$ to emphasize that the baseline data are fixed prior to any mixture sampling and to stress our use of conditional likelihood.

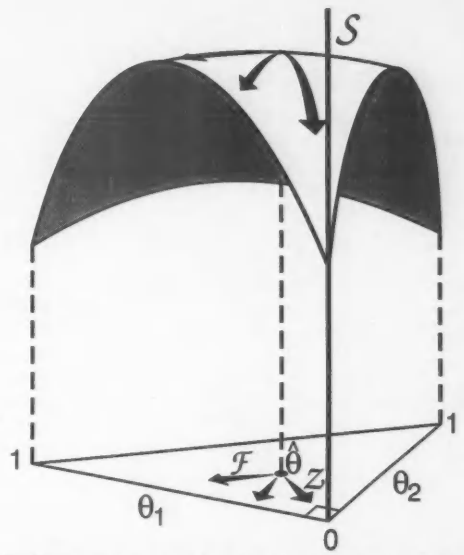

FIG. 2. Curvatures in various directions from the maximum point on a likelihood surface $\mathcal{S}$. Direction $\mathfrak{T}$ is that of steepest descent. The curvature in the direction of flattest descent, direction $\mathfrak{F}$, is used as a conservative utility measure of the data on which the likelihood surface depends.

The goal is now to rid ζ of its dependence on **y**. The key to attaining this goal is to note that **y** is sampled from a multinomial distribution based on the "unknowable" parameter Θ. The probability that a surface $\mathcal{S}$, and hence the curvature measure of that surface, ζ, is used in parameter estimation is the same as the probability that the mixed ocean sample **y** is obtained. To free ζ from its dependence on the mixed ocean sample, we average it over all possible mixed ocean fishery data:

$$(2) \quad \zeta_{\mathbf{X}} \equiv E_{\Theta}[\zeta(\mathbf{y}|\mathbf{X})]$$

where the expectation in equation (2) is taken over the multinomial density, with parameters **y** and Θ, corresponding to all feasible mixture samples.

As defined in equation (2), $\zeta_{\mathbf{X}}$ does not depend on mixed ocean samples. This was achieved, so it seems, at the expense of introducing explicit dependence of $\zeta_{\mathbf{X}}$ on the underlying Θ. Each mixture sample **y** has positive probability of occurring with an infinite number of mixing proportions. For this reason one cannot simply "solve" for the mixing proportions given the mixed ocean sample **y** (see Berger and Wolpert 1984 for further technical discussion). Ways of handling this problem are discussed in the Sampling over the True, but Unknown, Mixing Proportions section. In summary, however, the curvature measure in equation (2) defines a measure of utility based solely on baseline data.

Implementation Practicalities

Three subproblems must be solved in the process of calculating the curvature measure $\zeta_{\mathbf{X}}$. First, the flattest descent curvature of $\mathcal{S}$ at $\hat{\theta}$, $\zeta(\mathbf{y}|\mathbf{X})$, is evaluated for various parameter vectors **y**; next, the expectation (equation (2)) is taken; and

finally, the problem with sampling over the underlying mixing parameter is solved.

Calculating the Curvature $\zeta(\mathbf{y}|\mathbf{X})$

The curvature at the likelihood surface peak $\mathcal{S}(\hat{\theta})$ describes the rate of drop-off. The altitude drop in the direction $\hat{\theta}$ to θ is given by the (positive) difference $\mathcal{S}(\hat{\theta}) - \mathcal{S}(\theta)$. Using a Taylor series expansion and assuming that the likelihood function is sufficiently smooth near the peak gives

$$(3)\quad \mathcal{S}(\hat{\theta}) - \mathcal{S}(\theta) = -\tfrac{1}{2}(\hat{\theta}-\theta)^T\mathbf{H}(\hat{\theta})(\hat{\theta}-\theta) + O\|\hat{\theta}-\theta\|^3,$$

where $\mathbf{H}(\hat{\theta})$ is the Hessian matrix of second partial derivatives of $\mathcal{S}(\theta)$ with respect to the θ_i's, evaluated at the maximum point $\hat{\theta}$. The quadratic form in the difference vector $\hat{\theta}-\theta$ of equation (3) serves as the second order approximation to $\mathcal{S}(\hat{\theta})-\mathcal{S}(\theta)$.

The definition of $\zeta(\mathbf{y}|\mathbf{X})$ as the curvature in the direction of flattest descent nicely lends itself to the theory of quadratic forms (Noble and Daniel 1977). The theory says that the direction of flattest descent is the same as that of the eigenvector associated with the smallest eigenvalue of the matrix $-\frac{1}{2}\mathbf{H}(\hat{\theta})$; this matrix is nonnegative definite because the difference (3) must be nonnegative in any direction if $\mathcal{S}(\hat{\theta})$ is indeed the surface maximum. $\zeta(\mathbf{y}|\mathbf{X})$ is then defined as that minimal eigenvalue and the problem of calculating $\zeta(\mathbf{y}|\mathbf{X})$ is reduced to that of computing the smallest eigenvalue of the Hessian matrix $-\mathbf{H}(\hat{\theta})$. This can be accomplished using the inverse power method (Press et al. 1986).

An Approximation

The prospect of taking the expectation (2) of the $\zeta(\mathbf{y}|\mathbf{X})$ is daunting. In practice, the mixture sample taken is as large as possible (constrained by money and logistics), but the size varies each season. Calculating the probabilities of all potential samples within the expectation, although straightforward, would require a large amount of computer time. Decisions would also have to be made regarding which sample sizes to include and exclude in the expectation. In general, direct computation of the expectation for practical applications is expensive. Here we introduce an approximation that makes it unnecessary.

If a large enough mixture sample can be gathered, then we can approximate the expectation (2). The Hessian is

$$(4)\quad \mathbf{H}(\hat{\theta}) = -\sum_{g=1}^{G}\frac{y_g x_{gi} x_{gj}}{\left[\sum_{s=1}^{S} x_{gs}\hat{\theta}_s\right]^2};\ i, j = 1, \ldots, S.$$

As the mixture sample size N becomes large, two simplifications occur. First, the genotype vector component y_g is closely approximated by a sum:

$$(5)\quad y_g \cong N\sum_{s=1}^{S} x_{gs}\Theta_s \text{ for } N \text{ large.}$$

That is, the number of samples with genotype g in the mixture sample approaches the expected number with genotype g in the mixture of size N as the sample size gets large. Second, as N increases the MLE $\hat{\theta}$ converges to the true stock proportion vector Θ,

$$(6)\quad \hat{\theta} \cong \Theta \text{ for } N \text{ large.}$$

In fact for sufficiently large N, the maximum likelihood estimate $\hat{\theta}$ is strongly consistent (Redner and Walker 1984).

The asymptotic expressions (5) and (6) provide a limiting value of the Hessian matrix in equation (4) for mixture samples of size N, for large N:

$$(7)\quad \mathbf{H}(\hat{\theta}) \cong \mathbf{H}(\Theta) \cong -N\sum_{g=1}^{G}\frac{x_{gi}x_{gj}}{\sum_{s=1}^{S} x_{gs}\Theta_s}$$

When N is large, equation (7) completely determines (to second order and to within a multiplicative factor — see equation (3)) the likelihood surface corresponding to a mixture sample of size N. We now denote the likelihood for a mixture of size N by $\mathcal{S}_N$. The Hessian of $\mathcal{S}_N$ will be denoted by $\mathbf{H}_N(\Theta)$ and its curvature measure (minimum eigenvalue) by $\zeta_{\mathbf{X}}(\Theta,N)$.

Every element in the Hessian matrix (7) is multiplied by the mixture sample size N. Linear algebra shows that if λ_N is an eigenvalue of $\mathbf{H}_N(\Theta)$, then

$$M\,\lambda_N/N$$

is an eigenvalue of $\mathbf{H}_M(\Theta)$ for the same baseline data and stock proportion vector. This means that if M and N are different sized mixed ocean samples, then the curvatures are related by

$$(8)\quad \zeta_{\mathbf{X}}(\Theta, N) = \frac{N}{M}\zeta_{\mathbf{X}}(\Theta, M)$$

when M and N are large enough. A corollary to (8) is that, not surprisingly, larger sample sizes yield better (with respect to curvature) maximum likelihood estimates.

From equation (8) it is clear that $\zeta_{\mathbf{X}}(\Theta,N)$ is proportional to sample size. Thus, we define $\zeta_{\mathbf{X}}(\Theta)$ by

$$(9)\quad \zeta_{\mathbf{X}}(\Theta) \equiv \frac{\zeta_{\mathbf{X}}(\Theta, N)}{N}$$

to obtain a definition of curvature measure independent of sample size, where we assume that N is large enough for (7) to be valid. Since sample sizes of over 1000 fish have typically been collected for GSI analyses of chinook fisheries (Gall et al. 1989; Shaklee et al. 1989), it is likely that (7) will be a valid approximation in practice.

Sampling over the True, but Unknown, Mixing Proportions

If the explicit form of $\zeta_{\mathbf{X}}(\Theta)$ could be obtained, then it might also be possible to use analytic techniques to extract its minimum value over the Θ parameter space. In practice a closed form expression is difficult to find and some sampling strategy of the Θ parameter space must be used when searching for, say, the global minimum of $\zeta_{\mathbf{X}}(\Theta)$. Methods are available for locating minima of such complicated functions (e.g. Gill et al. 1981).

In the simulation described below, systematic discrete sampling over Θ space is used to gather information about the comparative curvature function $\zeta_{\mathbf{X}}(\Theta)$. How information regarding $\zeta_{\mathbf{X}}(\Theta)$ is used to quantitatively characterize the "utility" of the baseline data $\mathbf{X}$ depends upon what estimator properties are desired. For example, the minimum of $\zeta_{\mathbf{X}}(\Theta)$ over all Θ is the most conservative utility measure of baseline data $\mathbf{X}$. However, this minimum might be achieved only under highly unusual circumstances. An alternative measure of overall baseline utility might be obtained by averaging $\zeta_{\mathbf{X}}(\Theta)$ over the entire feasible space of Θ or some smaller realistic range if there is a priori information available about fishery composition or if some stocks are more important than others for management

TABLE 2. Baseline frequencies for a three-stock fishery. Genetic data is from a diallelic locus. Mating within stocks is assumed to be random with respect to this locus. The A allele has frequency p_j in stock j while the frequency of allele a is $1-p_j$.

		Stock 1	Stock 2	Stock 3
Genotype	AA	p_1^2	p_2^2	p_3^2
	Aa	$2p_1(1-p_1)$	$2p_2(1-p_2)$	$2p_3(1-p_3)$
	aa	$(1-p_1)^2$	$(1-p_2)^2$	$(1-p_3)^2$

purposes. The decision to use the global minimum or overall average curvature as a measure of baseline data quality depends upon whether one defines "utility" of baseline data with respect to worst-case or average estimator performance. Other choices are, of course, possible as well.

Sampling Issues

All data are not created equal. One set of baseline data, while being a good discriminator (with respect to curvature) may be quite difficult to sample in the mixture. Another set may not have as high a comparative quality measure but may be readily obtainable. The approximations given above provide a rough guide for estimating a mixture sample size with the same curvature quality. Thinking of $\mathbf{X}$ as representing the data of a single genetic locus, the comparative curvature measure, $\zeta_{\mathbf{X}}$, can be thought of as the "locus utility per mixture sample" and $N\zeta_{\mathbf{X}}$ as the (total) discriminatory utility of locus $\mathbf{X}$ for a mixture sample of size N.

Suppose that locus $\mathbf{X}$ ranks highly in comparative discriminating power but is very expensive to sample, and that locus $\mathbf{Z}$ ranks lower than $\mathbf{X}$ but is much cheaper per sample to obtain. The operational decision of how to best spend funds and time sampling $\mathbf{X}$ and $\mathbf{Z}$ in the mixture can be based on the comparative curvature measures for each data set. In fact, if each mixture sample of locus $\mathbf{X}$ has a cost (including time) of $D_{\mathbf{X}}$ dollars, then a measure of discrimination gain per dollar is

$$\frac{\zeta_{\mathbf{X}}}{D_{\mathbf{X}}} .$$

Standard techniques can employ the values

$$\frac{\zeta_{\mathbf{X}}}{D_{\mathbf{X}}}$$

for each locus to determine the optimal sample size for a specified level of overall utility.

Numerical Studies

We now describe methods and results of a numerical study of the comparative curvature measure $\zeta_{\mathbf{X}}(\Theta)$. The study is divided into two parts: (1) calculation of $\zeta_{\mathbf{X}}$ and (2) determination of errors in maximum likelihood estimation for some fisheries simulated from the same baseline data $\mathbf{X}$. We then compare the results.

We concentrate on a simple fishery consisting of three stocks and consider either one or two loci. For the case of a single locus, the frequencies of alleles A and a in stock j are p_j and $1-p_j$, respectively. Under the assumption of random mating within stocks, the three diploid genotype frequencies within stock j are given by their Hardy-Weinberg proportions p_j^2, $2p_j(1-p_j)$, and $(1-p_j)^2$. The 3 by 3 matrix of these genotype frequencies (Table 2) is the baseline data, $\mathbf{X}$, to be assessed for utility. When two diallelic loci are used, we make the additional assumption that there is no linkage disequilibrium. The nine two-locus genotype frequencies in stock j are found by multiplying each of the one-locus genotype frequencies.

TABLE 3. Average and minimum curvature measures for baseline data generated by one-locus two-allele gene frequency data. ("Avg_Θ" refers to the average value and "Min_Θ" refers to the minimum value of $\zeta_{\mathbf{X}}(\Theta)$ over Θ's sampled.)

p_1	p_2	p_3	$\text{Avg}_\Theta(\zeta_{\mathbf{X}})$	$\text{Min}_\Theta(\zeta_{\mathbf{X}})$
0	0.6	1	1.08182	0.41101
0	0.4	1	1.08178	0.41101
0	0.2	1	0.75720	0.21874
0	0.8	1	0.75716	0.21874
0	0.4	0.8	0.39133	0.20102
0.2	0.6	1	0.38569	0.20102
0.2	0.8	1	0.25714	0.12174
0	0.2	0.8	0.25713	0.12174
0	0.6	0.8	0.19035	0.10080
0.2	0.4	1	0.19035	0.10080
0	0.2	0.6	0.12673	0.04217
0.4	0.8	1	0.12654	0.04217
0	0.4	0.6	0.09234	0.03846
0.4	0.6	1	0.09234	0.03846
0.2	0.6	0.8	0.06963	0.06173
0.2	0.4	0.8	0.06963	0.06173
0.6	0.8	1	0.04333	0.01389
0	0.2	0.4	0.04332	0.01389
0.2	0.4	0.6	0.01873	0.01383
0.4	0.6	0.8	0.01873	0.01383

TABLE 4. Average and minimum curvature measures for baseline data generated by gene frequency data from two diallelic loci. ("Avg_Θ" refers to the average value and "Min_Θ" refers to the minimum value of $\zeta_{\mathbf{X}}(\Theta)$ over Θ's sampled.)

Locus 1: p_1 p_2 p_3 Locus 2: q_1 q_2 q_3				$\text{Avg}_\Theta(\zeta_{\mathbf{X}})$	$\text{Min}_\Theta(\zeta_{\mathbf{X}})$
(i)	0	0.4	1	1.56734	0.83695
	0	0.4	1		
(ii)	0	0.6	1	1.56736	0.83695
	0	0.6	1		
(iii)	0.2	0.4	0.8	0.47065	0.42142
	0.2	0.6	0.8		
(iv)	0.2	0.4	0.8	0.87123	0.66039
	0.2	0.8	0.6		
(v)	0	0.4	1	1.16232	0.56635
	0.4	0.6	0.8		
(vi)	0	0.4	1	1.55718	0.87867
	0	0.8	0.6		
(vii)	0	0.4	1	1.19939	0.62628
	0.6	0.4	0.8		

Calculation of the Curvature Measure

For each set of one- or two-locus baseline frequencies, $\mathbf{X}$, a grid of Θ space is formed and $\zeta_{\mathbf{X}}(\Theta)$ is evaluated at each Θ. Recall that $\zeta_{\mathbf{X}}(\Theta)$ is the smallest eigenvalue of the Hessian matrix (7) produced from the baseline data. To avoid difficulties on boundaries of the simplex of feasible Θ values, curvature calculations are done for proportion vectors that include positive contributions from all three stocks, i.e., we sample from the space $\{\Theta: \Theta_i > 0, i=1,2,3\}$. Interior values (19 702) of Θ

are sampled with an increment length of 0.005. If the inverse method did not converge within a reasonable number of iterations, the point was not sampled. Information leading to the mean, sum of squares, and minimum value of the curvature measure was recorded for the sampled points.

From this output, an assessment was made of the overall quality of the baseline data **X** in two ways. The quality of baseline data **X** was assigned (1) the average value of the minimum curvature value found through sampling the Θ space or (2) the value of the average curvature measure for the points sampled. Table 3 is a ranked list of the two quality measures for several sets of diallelic one-locus, three-stock baseline data. Table 4 presents the average and minimum curvatures for some diallelic two-locus, three-stock baseline data sets. Note that a different ordering may be found if the space of possible Θ were restricted to some subregion of the feasible simplex. We expect highest discriminatory power when the $\{p_i\}$ are well separated (e.g. $p_1 = 0$, $p_2 = 0.4$, $p_3 = 1$) and this appears to be the case. However, there is also a significant effect on discrimination based upon the location of the (across stock) average frequency. This latter observation is given full discussion below.

Simulated Fisheries and Error in Estimation

To examine the utility predicted by the curvature measure $\zeta_{\mathbf{X}}(\Theta)$, we used several identical baseline data sets and pseudo-randomly generated mixture samples of $N = 1000$ one- or two-locus diploid genotypes (fish) for each of 105 values of Θ. The Θ vectors were chosen to lie uniformly spaced (step size of 0.0165) in the interior of the feasible simplex as done above in the calculation of the overall curvature measure. For each mixture fishery, the maximum likelihood estimates, $\hat{\theta}$, were computed using the EM algorithm and compared with the original stock proportions. The average and range of errors between the actual mixture proportion and the estimate over all Θ's sampled are shown in Fig. 3.

We performed a two-fixed-factor analysis of variance, with one-locus baseline data sets and the 105 Θ values used above as the fixed factors, in order to estimate the contribution of our pseudo-random sampling procedure to the range of errors in estimation. One hundred pseudo-random mixture samples were generated for each combination of baseline and proportion vector and the error in maximum likelihood estimation computed for each simulation. The ANOVA showed that both the contributions of the baseline data sets and the systematically sampled Θ's to variation in estimation error are highly significant, at the 0.01% level, compared with the variance in our mixture sampling process.

Wood et al. (1987) performed a similar study on the effects of mixture sample size on estimation error. For a fixed Θ, they found the distribution of "angular deviations" in likelihood estimation for various simulated fisheries. The results obtained here are consistent with theirs even though we use a different definition of deviation and deviations are averaged over many values of Θ.

Discussion

High Average Curvature and Low Overall Estimation Errors

What is the relationship between the theoretically derived measure of baseline quality, $\zeta_{\mathbf{X}}$, and the performance of

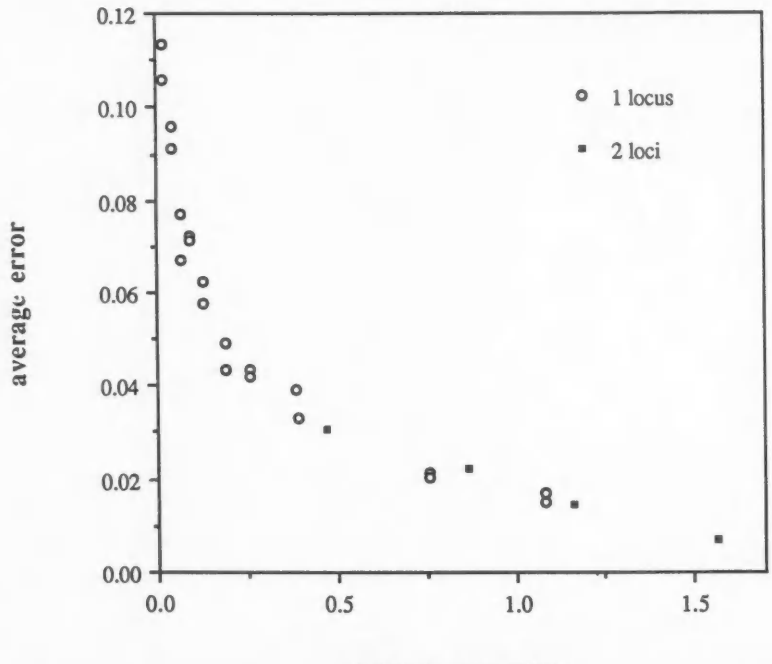

FIG. 3. Average absolute estimation error generated in simulations of different baseline data sets versus the average curvature value of the same baseline data. Open circles are one-locus baseline sets; solid squares are two-locus baseline sets.

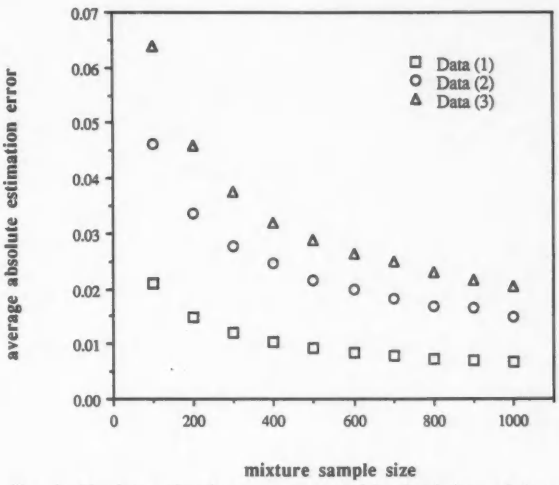

FIG. 4. Absolute estimation error generated in simulations of three baseline data sets over a range of mixture sample sizes.

Data (1) is the two-locus baseline 0 0.4 1
0 0.4 1;
Data (2) is the one-locus baseline 0 0.4 1;
Data (3) is the two-locus baseline 0.2 0.4 0.8
0.2 0.8 0.6.

maximum likelihood estimation in fisheries derived from the same baseline? As Fig. 3 shows, there is an almost functional relation between the overall utility measure, $\text{Avg}_{\Theta}(\zeta_X)$, and the overall error in estimation. Higher assessments of data utility, using the criterion of average curvature, correspond to a smaller error in maximum likelihood estimation on average for a fixed mixture sample size. We see from Table 3 that there is no change in overall quality ranking if the measure used is the overall nonzero minimum. However, the average curvature provides for a broader range of values. The inverse relation between utility and error holds despite excluding values of zero minimum curvature from the averaging process.

Other values found in Table 3 highlight the consistency of the utility measure between "similar" baseline data sets. This consistency is borne out in the estimation errors of fisheries produced from the same data (Fig. 3). For example, the baseline sets generated from {0.2, 0.4, 0.8} and {0.2, 0.6, 0.8} have nearly identical average curvature values while the mean estimation errors in fisheries derived from them differ in relative magnitude by no more than 15%. This was the worst case.

Because quality measures are directly comparable for the same size mixtures, average estimation errors found for different data sets should vary consistently over mixture sample sizes. To test this prediction we calculated average estimation errors based on simulated mixture samples ranging in size from 100 to 1000 for three baseline data sets:

Data (1) - Two diallelic loci with frequencies $p_1 = 0$, $p_2 = 0.4$, $p_3 = 1$ at locus 1 and frequencies $q_1 = 0$, $q_2 = 0.4$, $q_3 = 1$ at locus 2. $\text{Avg}_{\Theta}(\zeta_X) = 1.57$ for this baseline.

Data (2) - One diallelic locus with frequencies $p_1 = 0$, $p_2 = 0.4$, $p_3 = 1$. $\text{Avg}_{\Theta}(\zeta_X) = 1.08$ for this baseline.

Data (3) - Two diallelic loci with frequencies $p_1 = 0.2$, $p_2 = 0.4$, $p_3 = 0.8$ at locus 1 and frequencies $q_1 = 0.2$, $q_2 = 0.8$, $q_3 = 0.6$ at locus 2. $\text{Avg}_{\Theta}(\zeta_X) = 0.87$ for this baseline.

The results, this time computed from 4851 evenly spaced interior values of Θ, are plotted in Fig. 4. It is apparent from this data that ratios of the average errors for different mixture sizes are practically constant for all sizes used. The curvature measure does indeed distinguish baseline data quality over a wide range of mixture sample sizes.

Variation and Location Determine Average Estimation Error

We stated in the Calculation of the Curvature section that the performance of maximum likelihood estimation depended not simply on the variation in baseline frequencies between stocks, but also on the location of the average frequency. Because of symmetry, location can be measured relative to the frequency extremes 0 and 1. As a specific example, consider three one-locus data sets (A) {0, 0.2, 0.6}, (B) {0.4, 0.8, 1}, and (C) {0.2, 0.6, 0.8}. A priori, one expects that data sets (A) and (B) will have greater utility than (C) since each contains a fixed allele (Brodziak 1987). The variance for all three sets is 0.093. The average frequency is 0.27 for baseline (A), 0.73 for (B), and 0.53 for (C). Data sets (A) and (B) have curvature value 0.127 while baseline (C) has value 0.070. Consequently, our results lead to the prediction that the overall error in maximum likelihood estimation should be greatest for baseline data (C) even though its variation in frequencies is exactly the same as data sets (A) and (B). Also note that the average frequency for (B) is exactly the same distance from 1 as the average for (A) is from 0 and their respective estimation errors are comparable.

To summarize, the utility (with respect to maximum likelihood methods) of a locus depends on both the magnitude of the variation among populations and the location, relative to 0 and 1, of the center of that variation. The magnitude of variation may predominate in determining the quality of a data set but it is not the only factor that has an effect. The curvature measure takes variation, location, and possibly other distributional factors into account when quantifying the utility of a baseline data set. This is important, because the actual maximum likelihood process also takes these factors into account during the estimation of mixing proportions.

Wood et al. (1987) also noticed the effect of the mean frequency on the curvature of the likelihood surface. In their analysis, they generated three-stock baseline data sets of nine independent loci. Within a baseline data set, every locus shared the same frequency distribution. One example had two baseline data sets with the same Nei genetic distance (Nei 1972) but different median allele frequencies. Over three stocks, at each locus for the two baseline sets, the data were {0.02, 0.12, 0.203842} and {0.442184, 0.5, 0.557816}. The second baseline set has a much flatter likelihood surface than the first (see their figures 2B and 2D). By the conclusions of the previous paragraph, the shape difference is due partly to an inward shift in average (or median) frequency and, to a more substantial extent, to a reduction in variance. However because the Nei distance is equal for both data sets, it does not detect any difference in the shape of the likelihood surface between these data sets.

In their other example, two baseline sets were generated with the same between-stock frequency differences but different medians. The frequencies were {0.02, 0.12, 0.22} and {0.4, 0.5, 0.6}. The median values match those in the Nei's distance example. These two baseline sets have equal variances but different means (the second set has median closer to 0.5) and the respective likelihood surfaces are also different (the likelihood surface for the second data set is flatter — see their figures 2A

and 2C). The difference in likelihood surface shape is not as dramatic as in the Nei's distance example. We can now explain why there is a difference between likelihood surface curvatures in each example as well as why that difference is more pronounced in the Nei's distance example.

These examples also show that a utility measure based on Nei's genetic distance can reveal less information about likelihood estimation than simple variance based measures. However, variance based measures cannot account for the location of the center of variation. Whether or not the variance in a baseline data set is alone a decent predictor of its utility is critically dependent on the sensitivity of the associated likelihood surface to the location of the center of its underlying data distribution. The curvature measure introduced in this paper takes all of these factors into account in a unified and consistent manner.

How do One-Locus Utilities Combine?

Examination of Tables 3 and 4 shows that the utility of two-locus baseline sets is not independently determined by the component one-locus utility measures. In fact the curvature measures for different baseline sets which have identical unordered one-locus frequency distributions, such as data sets (iii) and (iv) in Table 4, are noticeably different. This suggests that the magnitude of increase in estimation accuracy, when estimates are based on two loci, depends on how the loci vary together across stocks. The same data sets show that data utility is greatly increased when two loci, of relatively fair individual utility, are used in tandem.

Baseline sets (v)–(vii) in Table 4 illustrate how loci of relatively poor individual utility affect the utility measure of an individually high utility locus. Again, there is a synergism between the two individual frequency distributions. These three data sets also emphasize how the synergism between distributions of individual locus frequencies among stocks is reflected in the variance of utility measures. However, all three values are consistently higher than the utility measures for the individually mediocre loci comprising baseline sets (iii) and (iv). See Table 3.

Overall Curvature Quality as a Guide to Resource Allocation

If mixture proportions are to be estimated based on a mixture sample of fixed size, then the curvature measure and simulation results above can guide in choosing the best sampling scheme. In particular, should one or two loci be sampled from each fish? There are two important messages from Figs. 3 and 4. First, the relative magnitude of average estimation errors between different quality data sets remains constant over sample size; second, for a fixed sample size, the absolute gain in estimation accuracy decreases with curvature value.

These two observations have practical implications for sampling effort. If the sample size to be obtained is "large" then fewer loci per fish can be sampled with a small absolute decrease in accuracy. For example, the average curvature measures for the one locus counterpart of baseline data (ii) in Table 4 has curvature measure 1.08 while the two locus baseline data set has measure 1.57. There is a consistent three-fold difference in average estimation error for the 1 and 2 locus data sets over all sample sizes. But despite their relative differences, the overall gain in estimation accuracy when sampling twice as many loci in the mixture sample, for 1000 fish, is less than 1%. On the other hand, if the mixture sample size is constrained to be "small," the loss in accuracy resulting from sampling one locus from each of 100 fish, rather than two loci, is 2.5% on average. Depending on the application, a 2.5% loss in accuracy may represent too large a cost and both loci should be sampled.

If the limiting resource is the number of loci that may be sampled, rather than the number of fish, then one might consider using the overall curvature measure to decide whether it would be more effective to sample one locus from each of N fish or two loci from each of $N/2$ fish. It was previously mentioned that curvature utility measures are directly comparable for the same mixture sample size while there is a theoretical relation (see equation (8)) between different sample size specific curvature values. Applying this relation to error prediction, when equal numbers of loci are sampled in each fishery the one-locus baseline generated from the frequency distribution {0, 0.4, 1}, with average curvature 1.08, should have smaller overall estimation error than that found from the two-locus baseline frequencies generated by those in Table 4 (i), with quality value

$$\frac{N/2}{N}(1.57) = 0.785.$$

The simulation results in Fig. 4 indicate that the average estimation error found using two-locus samples from 500 fish is 0.0093 while when using one-locus samples from 1000 fish, the comparable estimation error is 0.015, contrary to prediction. Thus although the average curvature measure can rank the utility of one- and two-locus samples for a fixed sample size of fish, the nonlinear relation between curvature measure, sample size, and estimate error precludes the simple use of a data set's curvature value in choosing the best sampling allocation of a fixed number of loci.

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A Genetic Mixture Analysis for use with Incomplete Source Population Data

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While anadromous salmonids reproduce in fresh water, most harvests occur at sea. Effective genetic management requires knowledge of the stock (source population) composition of the harvest. This is accomplished with genetic stock identification (GSI), which compares the genotypes of harvested fish with those of freshwater stocks, assuming that all candidate stocks are identified and that their allele frequencies are known exactly. We develop methods that: (1) allow for sampling error in allele frequencies of candidate stocks, and (2) evaluate the possibility of unsampled contributing stocks. Composition analysis for chinook salmon (*Oncorhynchus tshawytscha*) collected for the Bonneville Dam egg bank program in 1980 and 1981 shows that about 10% of both harvests were from the Deschutes River and about 90% from the Hanford Reach area. Contributions from lower Columbia and Snake River stocks or from unidentified sources were limited.

Alors que les salmonidés anadromes se reproduisent en eau douce, la plus grande partie du prélèvement se fait en mer. Une gestion génétique efficace exige que l'on connaisse l'origine des stocks qui composent les captures. On procède pour cela à l'identification génétique des stocks, qui compare le génotype des poissons capturés à celui des stocks d'eau douce, en posant que tous les stocks candidats sont identifiés et qu'on connaît exactement les fréquences des allèles au sein de ces stocks. Nous mettons au point des méthodes qui (1) font place à l'erreur due à l'échantillonnage dans les fréquences des allèles des stocks candidats, et (2) évaluent la possibilité que certains stocks n'aient pas été échantillonnés. L'analyse de l'origine des saumons (*Oncorhynchus tshawytscha*) quinnats recueillis en 1980 et 1981 dans le cadre du programme de la banque d'oeufs du barrage de Bonneville montre que 10 % environ des prises des deux années provenaient de la rivière Deschutes et environ 90 % de la région de Hanford Reach. La contribution des stocks du cours inférieur du Columbia et la rivière Snake et celle des stocks d'origine inconnue étaient limitées.

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The biological management of wild populations of anadromous salmonids (salmon and sea-run trout) in the Pacific Northwest has always been a difficult proposition. Salmon and steelhead reproduce in discrete, freshwater localities to which their offspring return with high fidelity. There is evidence for genetic and morphological differentiation of stocks separated by small geographic distances (e.g. Ricker 1972). These species, however, exist in discrete freshwater populations only during juvenile development and spawning runs; the fish spend the remainder of their lives (generally 2–5 yr) in the ocean. Harvesting occurs primarily at sea or near the mouths of major river systems, where the catch may include fish from a large number of sources.

For a number of reasons, it is important to assess the proportionate contributions of different stocks to these harvests. First, although Pacific salmon can travel several thousand miles at sea (French et al. 1976; Burgner 1980), they are considered to be a resource of the state (or country) in which their home stream is located. Regulatory agencies must address the question: "Who is catching whose fish, and what compensation is due as a consequence?" Second, recent court decisions enforcing long-standing treaties have mandated adequate protection of certain upriver stocks to meet Native American quotas (Fraidenburg and Lincoln 1985). Third, human activities, particularly increased fishing pressure and the construction of hydroelectric power dams, have contributed to a substantial reduction in abundance of salmon and steelhead since World War II, and there is increasing concern over the status of endangered wild stocks (MacNeil and Himsworth 1980; Wahle and

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Pearson 1984; Williams 1989). Fourth, hatchery production of salmonids in the Pacific Northwest has been a substantial enterprise for decades, and it is important to evaluate the relative contributions of hatchery and wild fish to the harvest (Mathews 1980; Washington 1985; Vreeland 1986).

The problem is to identify the natal streams of fish caught in the commercial and sport fisheries. Considerable efforts have been focused on this matter over the last quarter century. Tagging has provided valuable insight into homing and migratory behaviors, and extensive coded-wire tag studies involving hatchery stocks are currently under way (Fraidenburg and Lincoln 1985; Johnson 1990). Such studies are labor intensive and expensive, however, and must be repeated in toto each generation to obtain new information. Furthermore, tagging wild stocks is an especially difficult endeavor.

Morphometric and meristic data can be of some use in stock identification, but such characters typically exhibit broad overlap between stocks and are sensitive to environmental conditions (Taning 1952; Barlow 1961; Fowler 1970; Clayton 1981). More recently, attention has focused on a variety of bioassay methods (Ihssen et al. 1981). Promising results have been obtained with scale pattern analyses (Henry 1961; Major et al. 1972; Jarvis et al. 1978; Cook 1982; Bigler 1989), but these characters are also subject to environmental modification and are not always temporally stable (Ihssen et al. 1981). Natural parasites in some salmon species are restricted to stocks from certain areas (Margolis 1982; MacKensie 1983; Bailey 1984), and they are routinely used in stock identification of sockeye salmon (Wood et al. 1989).

The last decade has seen the emergence of a powerful new method, genetic stock identification (GSI), the first step of which is to characterize potential source populations from archived allele frequency data. The body of electrophoretically generated data that has been gathered on Pacific salmon since the early 1970's probably exceeds that for any organism except *Homo sapiens* and *Drosophila*. Allele frequencies have been surveyed in well over 100 chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*O. mykiss*) populations, and smaller data sets are available for chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*), and sockeye (*O. nerka*) salmon (e.g. Utter et al. 1973; Aspinwall 1974; Kristiansson and McIntyre 1976; Grant et al. 1980; Utter et al. 1984; Parkinson 1984; Beacham et al. 1987; Gharret et al. 1987; Wehrhahn and Powell 1987; Utter et al. 1989). Genetic differences among stocks are typically quantitative rather than qualitative, representing variation in frequencies of shared alleles rather than fixed allelic differences. It is not generally possible to allocate particular fish to their natal streams with certainty, so we cannot convincingly answer the question: "Whose fish is this fish?" We can, however, use likelihood analysis to estimate the fractions of any given mixed harvest that have come from the different source populations, by employing data for up to 30 polymorphic loci (Milner et al. 1981, 1985; Beacham et al. 1987; Utter et al. 1987; Wood et al. 1987). Several studies have demonstrated accuracy and precision for the composition estimates, provided the genetic (Hardy-Weinberg) and statistical (mixtures of multinomials) assumptions of the model are met (Milner et al. 1981; Fournier et al. 1984; Beacham et al. 1985; Millar 1987; Wood et al. 1987; Pella and Milner 1987).

Two of these assumptions, however, have been adopted more for convenience than biological realism, and they impose potentially serious limits on the usefulness of current GSI methods. The first limitation is that the allele frequencies of the stock populations (the baselines) are usually treated as parameters. They are always estimates, of course, often small sample estimates. Fournier et al. (1984) and Pella and Milner (1987) have discussed the use of 'bootstrap' techniques to gauge the sampling variation in the analysis. The second limitation is an absolute requirement of baseline data on all potential source populations, a necessity that is almost impossible to meet in practice. In some cases — for example, in many areas of Alaska and Canada — logistic considerations preclude sampling remote streams. In other cases, the number of potentially discrete spawning populations is simply too large to sample exhaustively; hence, it is difficult to determine whether all relevant populations have been sampled. While inadequate in many cases, these two assumptions are rationalized as necessary; they render tractable an analysis of multi-locus data for 100 or more candidate source populations.

Our broad objective here is to replace the standard likelihood estimates (conditioned on acceptance of the candidate source populations as an exhaustive list and their allele frequencies as known withour error) with an unconditional set of estimates. We treat the allele frequencies from the source populations as sample estimates of their unknown parametric (population) values, a device that permits a number of useful extensions of the standard analysis. We begin by outlining a statistical test of the hypothesis that the harvest is really a sample from a single panmictic gene pool, either one of those represented by a baseline collection or one not currently represented by a sample. We then describe an approach that permits estimation and testing of the proportional contributions of the several candidate stocks, both those represented by baseline data and those not represented. We show that while estimated baseline allele frequencies provide considerable resolution on the stock proportions, they are not essential for determining whether the harvest is actually a mixture of stocks. We can explicitly allow for unsampled stocks. A simple extension permits easy handling of missing data for particular individuals or source populations.

Finally, we apply these procedures to provide unconditional estimates of the proportionate contributions of various source populations to mixtures of chinook salmon. Chinook salmon are distributed over a broad geographic range (southern California to Japan). They are prized by both commercial and sport fishermen, and their propensity to cross state and national boundaries during their one to several years at sea makes them a challenging species to manage effectively. We begin with some carefully contrived mixtures of seven source populations, as an illustration that the analysis performs as advertised. We then turn to analyses of the 1980 and 1981 egg bank collections at Bonneville Dam. In recent years, spawning runs of chinook salmon have been estimated to be as much as 70% below optimal levels, due in large part to habitat loss, disruption of migratory routes, and increased fishing pressure (Fraidenburg and Lincoln 1985). Declining run sizes have highlighted the necessity of effective management strategies, and GSI techniques are currently being used to provide information toward this end. The goal of the egg bank collections was to enhance the upriver bright' portion of the run without intercepting fish from the endangered Snake and Salmon River stocks.

The results of the present analysis shed some light on a number of questions that cannot be addressed with the current GSI model. (1) What is the effect of treating the baseline frequencies as random variables instead of parameters known without error? (2) Under what circumstances can we reject the null hypothesis that the mixture contains only stock A (or only A and B, etc.)?

(3) Do we find any evidence that unsampled stocks contribute significantly to the egg bank harvest?

Genetic Mixture Analysis

Mixed Gene Pools

The theory that follows is based on three assumptions. (a) Allele frequencies vary among source populations. (b) While the harvest may be a mixed catch, each of the source populations is essentially a separate breeding pool. (c) Mating is genetically random within a source population. For Pacific salmon, (a) is known to be true, (b) is largely true as a consequence of the strong homing behavior, and (c) is probably an adequate approximation, based on general conformity of genotypic frequencies to Hardy-Weinberg expectations in many large data sets. Standard population genetics theory shows that if the harvest is a mixture, it will exhibit Wahlund effect, excesses of homozygotes and deficiencies of heterozygotes. Multiple-locus departures from panmictic equilibrium can be used to estimate both the relative contributions of the various source populations and their allele frequencies.

Consider first a codominant genetic locus (A) with $J = 2$ alleles (A_1 and A_2), and a set of I source populations contributing to the harvest in question. If the allele frequencies of the i-th source population ($i = 1, \ldots, I$) are denoted by p_{ij} and if the proportionate contributions to the mix are denoted by m_i ($i = 1, \ldots, I$), with $m_i \geq 0$ for all i populations and $\Sigma_i m_i = 1$, then the expected frequencies of genotypes from the i-th source population will follow the multinomial distribution with Hardy-Weinberg frequencies:

$$(1a)\quad f_i(A_jA_k) \equiv \begin{cases} p_{i1}^2 & \text{for } A_1A_1 \\ 2p_{i1}p_{i2} & \text{for } A_1A_2 \\ p_{i2}^2 & \text{for } A_2A_2, \end{cases}$$

while the corresponding expected frequencies of the harvest are:

$$(1b)\quad f_h(A_jA_k) \equiv \begin{cases} \Sigma_i m_i p_{i1}^2 & \text{for } A_1A_1 \\ 2\Sigma_i m_i p_{i1} p_{i2} & \text{for } A_1A_2 \\ \Sigma_i m_i p_{i2}^2 & \text{for } A_2A_2. \end{cases}$$

This is the multi-population version of the model in Makela and Richardson (1977), also used in the current GSI model (Milner et al. 1981, 1985; Fournier et al. 1984; Millar 1987; Pella and Milner 1987; Wood et al. 1987).

The essence of our new treatment is to compute the likelihoods of a series of population sampling models, using genotype counts both from the harvest and from some or all of the candidate source populations. The null hypothesis is the panmictic hypothesis (H_h) that the harvest is really a single Hardy-Weinberg gene pool, and the alternative hypothesis (H_I) is that the harvest is a mixture of I different gene pools.

No Source Population Data

Even in the absence of any baseline data, the two hypotheses can be evaluated, since each has a likelihood, given counts (N_{hjk}) of genotyeps (A_jA_k) from the harvest collection. Given unknown harvest population (p_{hj}) and source population (p_{ij}) allele frequencies, we can write:

$$(2a)\quad L(H_h \mid \text{harvest}) \propto (p_{h1}^2)^{N_{h11}}(2p_{h1}p_{h2})^{N_{h12}}(p_{h2}^2)^{N_{h22}}$$

$$(2b)\quad L(H_I \mid \text{harvest}) \propto (\Sigma_i m_i p_{i1}^2)^{N_{h11}}(2\Sigma_i m_i p_{i1} p_{i2})^{N_{h12}} \cdot (\Sigma_i m_i p_{i2}^2)^{N_{h22}}$$

By maximizing these likelihoods relative to their respective parameters, we can both estimate those parameters and compare the two models statistically. The estimates from the null hypothesis are straightforward, taking the familiar gene-counting forms:

$$(3)\quad \hat{p}_{h1} = \frac{2N_{h11} + N_{h12}}{2N_h} \text{ and } \hat{p}_{h2} = \frac{N_{h12} + 2N_{h22}}{2N_h},$$

where $N_h = N_{h11} + N_{h12} + N_{h22}$. Those for the alternative (mixture) hypothesis (H_I) must be obtained by iterative techniques discussed later.

Maximizing $L(H_I \mid \text{data})$ for the p_{ij} and m_i parameters simultaneously by standard quadrature methods is not attractive, because we are dealing with a very large number of parameters. There is, however, a simple and heuristically appealing method of obtaining the estimates, called the 'expectation maximization' (EM) algorithm (Dempster et al. 1977), also the basis of the GSI algorithm. The essence of the method is that as long as the transformation is monotonic, functions of maximum likelihood estimates are maximum likelihood estimates of those functions. Instead of dealing with the genotype frequencies, we can deal directly with allele frequencies and mixture proportions.

The EM algorithm uses estimates of the source population allele frequencies (p_{ij}'s) to estimate the population mixture fractions (m_i's) in the harvest, and then uses the m_i's to reestimate the p_{ij}'s. We iterate the process to convergence, a procedure that finds a local maximum of the likelihood function. We begin with an initial (arbitrary) set of mixture fractions ($m_i^{(0)}$) and allele frequency estimates ($p_{ij}^{(0)}$) for each population. We define a set of indicator variables (X_l), multinomially distributed, for the two-allele A-locus of the l-th individual, and set the probabilities equal to the Hardy-Weinberg equilibrium frequencies for the i-th population:

$$(4)\quad X_l = \begin{cases} 1.0 \text{ for } A_1A_1 \\ 0.5 \text{ for } A_1A_2 \\ 0.0 \text{ for } A_2A_2 \end{cases} \quad Pr(X_l \mid i) = \begin{cases} [p_{i1}^{(0)}]^2 & \text{for } A_1A_2 \\ 2p_{i1}^{(0)}p_{i2}^{(0)} & \text{for } A_1A_2 \\ [p_{i2}^{(0)}]^2 & \text{for } A_2A_2. \end{cases}$$

Using these initial values, we estimate the probability that the l-th individual belongs to the i-th population. Using Bayes' Theorem, we estimate the probability that an individual exhibiting X_l belongs to the i-th population from the prior probability, m_i, that the individual was drawn from that population and the probability, $Pr(X_l \mid i)$, that an individual drawn from that population would exhibit X_l:

$$(5)\quad Pr(i \mid X_l) = \frac{m_i^{(0)} Pr(X_l \mid i)}{\sum_{i=1}^{I} m_i^{(0)} Pr(X_l \mid i)} \quad i = 1, \ldots, I.$$

From the estimated values of the $Pr(i \mid X_l)$ for all I source populations and all N_h harvest individuals, we obtain new estimates of the mixture values as the average values of $Pr(i \mid X_l)$ over all N_h individuals in the harvest:

$$(6)\quad m_i^{(1)} = \frac{\sum_{l=1}^{N_h} Pr(i \mid X_l)}{N_h} \quad i = 1, \ldots, I.$$

To obtain updated estimates of the allele frequencies (p_{i1}'s) for

the i-th population, we compute the expected value of X_l for that population, merely the sum of the X_l, each weighted by the probability that it was drawn from the i-th population, $Pr(i \mid X_l)$. For the full set of populations, we have:

$$(7a)\quad p_{i1}^{(1)} = \frac{\sum_{l=1}^{N_h} X_l \, Pr(i \mid X_l)}{m_i^{(1)} N_h} \qquad i = 1, \ldots, I.$$

We substitute equation (7a) into equation (4), noting that $p_{i2} = 1 - p_{i1}$, and iterate the whole process, equation (4) →(5) →(6) →(7a) →(4) → . . ., to convergence of both the m_i's and the p_{ij}'s, representing a peak of the likelihood surface.

With only two alleles at one locus, there are only three genotypes; we do not have enough information to estimate all of the necessary parameters. The function (2b) is 'not identifiable.' To insure identifiability for several source populations, we need many genotypic classes; we need either baseline data from the source populations, or more alleles, or more loci. The extension to multiple alleles at the A-locus leads to the multinomial generalizations of equation (1a) to (2b) and to null hypothesis allele frequency estimates that are the corresponding generalizations of equation (3). The likelihood equations and panmictic allele frequency estimates are the obvious extensions of equation (2a) to (3). To obtain the mixture hypothesis values of the m_i's and the p_{ij}'s, we replace the scalar X_l in equation (4) to (7a) with a multiple-allele vector x_l, representing the genotype of the l-th individual. For a $(J + 1)$-allele locus, there are J positions in x_l. A four-allele example should suffice to show the scoring pattern and multinomial (Hardy-Weinberg) probabilities, an analogue of equation (4):

	X^T-vector	Prob	X^T-vector	Prob
	A_1A_1 [1.0 0.0 0.0]	p_{i1}^2	A_2A_3 [0.0 0.5 0.5]	$2p_{i2}p_{i3}$
	A_1A_2 [0.5 0.5 0.0]	$2p_{i1}p_{i2}$	A_2A_4 [0.0 0.5 0.0]	$2p_{i2}p_{i4}$
(8a)	A_1A_3 [0.5 0.0 0.5]	$2p_{i1}p_{i3}$	A_3A_3 [0.0 0.0 1.0]	p_{i3}^2
	A_1A_4 [0.5 0.0 0.0]	$2p_{i1}p_{i4}$	A_3A_4 [0.0 0.0 0.5]	$2p_{i3}p_{i4}$
	A_2A_2 [0.0 1.0 0.0]	p_{i2}^2	A_4A_4 [0.0 0.0 0.0]	p_{i4}^2.

The net result of using equation (8a) instead of equation (4) is that we obtain a final set of estimates for all the m_i's and for all the p_{i1}'s, p_{i2}'s, and p_{i3}'s, and can obtain the p_{i4}'s by subtraction. The more alleles we have, the more parameters we can estimate, but we will never have enough alleles at a single locus to complete the estimation and testing task for more than a very few baselines in the absence of genetic data from those source populations.

With multiple loci, we can accomodate more candidate source populations. The likelihoods for independent loci are simply multiplied across all K loci. The extension of equation (4) to (7a) to multiple loci requires only a lengthening of the vector x_l; for the k-th locus, a sector of length J_k is added for the $(J_k + 1)$ alleles at the locus. The total length of the vector is $J = \Sigma_k J_k$.

While the EM algorithm will climb the likelihood surface, there are many potential peaks. That peak actually climbed can depend on the initial estimates of the allele frequencies and m-values. It is not obvious how we should choose the initial estimates of allele frequencies, but in the absence of source population data, we could set all the initial m_i's equal:

$$(9)\quad m_i^{(0)} = 1/I,$$

and the p_{ij}'s close to the average p-values ($\hat{p}_{hj}$'s) of the harvest collection, obtained from equation (3). Wide exploration of the likelihood surface, however, accomplished with many different sets of starting values, is the best way to explore the likelihood surface. With numerous sources, we cannot realistically expect to evaluate all possibilities, and there is no absolute guarantee that we will find the highest peak of the surface.

Given the estimated values of the p_{ij}'s under both H_h and H_I and the estimated values of the m_i's under H_I, we wish to test whether there is any evidence for a mixture of gene pools in the harvest, or whether the data can be described adequately by a single, panmictic (Hardy-Weinberg) gene pool. Inserting the null hypothesis estimates of the p_{hj}'s into the multiple-locus, multiple-allele version of equation (2a), and the corresponding alternative hypothesis estimates of both the m_i's and p_{ij}'s into the multiple-locus, multiple-allele version of equation (2b), we construct an approximate χ^2-test of the null hypothesis, using the natural logarithm of the usual likelihood-ratio test criterion:

$$(10a)\quad \Lambda_{hI} = 2[\log L(H_I \mid \text{data}) - \log L(H_h \mid \text{data})] \sim \chi^2,$$

with $(I - 1)(J + 1)$ degrees of freedom, J allele frequencies (for a locus with $J + 1$ alleles) and one mixture fraction for each of $(I - 1)$ populations.

To this juncture, we have said nothing about how to choose the number of source populations, particularly in the absence of any additional source population data and in ignorance of whether the harvest is really a mixed catch. Unless there is some very definite value of I to be considered in advance, the best strategy is to start with $(I = 2)$ source populations for the alternative hypothesis (H_I), comparing this model with $(I = 1)$ for the null hypothesis ($H_h = H_1$), so that Λ_{12} is a χ^2 with $(J + 1)$ degrees of freedom. If Λ_{12} is significantly larger than zero, then we try $(I = 3)$, and so on until the next source population does not add anything statistically useful (significant) to our description of the genotypic proportions in the harvest. This amounts to a sequential partition of Λ_{hI}, which takes the form:

$$(11)\quad \Lambda_{hI} = \Lambda_{12} + \Lambda_{23} + \Lambda_{34} + \ldots,$$

where each of the separate components is approximately χ^2 with $(J + 1)$ degrees of freedom. Without some guidance concerning the mixture proportions or source population allele frequencies, we cannot realistically expect much resolution; it will generally prove difficult to extract more than one or two components unless they are very different genetically. While the problem can be explicitly solved even in the absence of baseline data, statistical resolution is quite limited. The fact that we can proceed without such data, however, has some interesting (and useful) implications, to which we return later.

There is one caveat that we should mention at this juncture. Any submodel of H_I that involves less than I separate populations is really a boundary solution of H_I with one or more of the $m_i = 0$. The log-likelihood test criterion Λ only approximates a χ^2-distribution for contrasts of submodels that are missing stocks. Wolfe (1971) has suggested that the approximation to χ^2 can be improved if one computes (in our terminology):

$$(10b)\quad \tilde{\Lambda} = c\Lambda \sim \chi_d^2,$$

where c and d are elaborate functions of the sample size, the numbers of stocks being considered and the dimension of the vector x_L. The best procedure for precise testing under these circumstances is still a matter under active discussion; we refer the reader to McLachlan and Basford (1987; Chap. 1) for a

thorough discussion of this problem. For our purposes here, it is sufficient to understand that Λ is an immediate function of the likelihood ratio test criterion, and that we can view it as χ^2-like. Precise tail probability levels are less important than the realization that in searching for additional stock population contributors to the harvest, we seek large changes in Λ, relative to the change in the number of parameters that must be estimated with additional sources. We shall retain the χ^2 terminology throughout, but with the explicit understanding that the degree of approximation is rough.

Source Population Data Available

The stock composition of the harvest can be better elucidated if additional data on the candidate source populations are used — that is, data obtained from individuals caught at those localities and genetically typed for the loci in question. The standard GSI algorithm uses these stock samples to establish the initial $Pr(X_l \mid i)$, but these values are not iterated further, thus conditioning the mixture estimates on the sample allele frequencies. The iterative sequence is then equation (4) → (5) → (6) → (5) → (6) → . . ., and so on. The difference here is that while we use the stock samples to set the initial $Pr(X_l \mid i)$ in equation (4), we iterate those values as the analysis proceeds, using both the stock sample and harvest data. In routine practice, source population samples are small enough (typically 50–100 individuals) that baseline allele frequencies are estimated with (sometimes considerable) error. While it may be convenient to treat these estimates as known parameters, doing so entails some risks. We may have more fish from a given source in the harvest (typically a large sample) than we have in the baseline sample, and a better strategy is to use all of the data at our disposal to estimate the allele frequencies. This unconditional estimation strategy is discussed but not implemented by Pella and Milner (1987).

There are now two classes of models, and their likelihood equations take the general forms:

$$(12a)\quad L(H_i \mid \text{data}) = L(H_i \mid \text{source } i + \text{harvest}) \cdot \prod_{\substack{i'=1 \\ i' \neq i}}^{I} L(H_i \mid \text{source } i')$$

$$(12b)\quad L(H_I \mid \text{data}) = L(H_I \mid \text{harvest}) \cdot \prod_{i=1}^{I} L(H_I \mid \text{source } i).$$

The null hypothesis class $\{H_i : i = 1, \ldots, I\}$ specifies that the mixed fishery is really a sample from just one of the source populations, and there are I separate versions of this hypothesis, one for each candidate source population. The terms in equation (12a) all take the same Hardy-Weinberg form as equation (2a), with the mixed catch treated jointly with the i-th source collection. For example, suppose the mixed fishery catch were a sample from the third source population. The analogue of equation (2a) for this pair of samples would take the form:

$$L(H_3 \mid \text{source } 3 + \text{harvest}) \propto$$

$$(13)\quad (p_{3h1}^2)^{N_{h11}+N_{311}} (2p_{3h1}p_{3h2})^{N_{h12}+N_{312}} (p_{3h2}^2)^{N_{h22}+N_{322}}$$

and the analogue of equation (3) would be:

$$(14a)\quad \hat{p}_{3h1} = \frac{2(N_{h11}+N_{311}) + (N_{h12}+N_{312})}{2(N_h+N_3)}$$

and

$$(14b)\quad \hat{p}_{3h2} = \frac{(N_{h12}+N_{312}) + 2(N_{h22}+N_{322})}{2(N_h+N_3)}$$

All $(I - 1)$ of the other source populations would be treated as separate Hardy-Weinberg gene pools, where the allele frequencies are estimated as in equation (3), with h replaced by i to indicate source population, rather than the harvest. This amounts to setting $m_3 = 1$ and all other m_i's $= 0$.

Under the alternative hypothesis (H_I), all of the m's are potentially positive, and we resort to an iterative fitting routine. Again, likelihood scoring methods are not attractive, and we employ an expanded EM algorithm. As before, we begin the iteration with estimates of the m_i's and p_{ij}'s, but this time we use the estimated source population allele frequencies for the initial $Pr(X_l \mid i)$ in equation (4). We can again use the initial m_i-estimates in equation (9), but the estimates obtained from the conditional treatment (GSI) make a better choice, presumably drawing us into the vicinity of one of the higher peaks, if not the highest, of the likelihood surface. While careful exploration of the possible m-value in that region of the parameter space is still desirable, we have provided a 'statistical anchor' for the analysis. With the values in equation (4), and using only the N_h individuals of the harvest, we compute equation (5) and (6). To obtain updated estimates of the source population allele frequencies (p_{i1}'s), we now incorporate information from the source populations, replacing equation (7a) with:

$$(7b)\quad p_{i1}^{(1)} = \frac{\sum_{n=1}^{N_i} X_{in} + \sum_{l=1}^{N_h} X_l Pr(i \mid X_l)}{N_i + m_i^{(1)} N_h} \qquad i = 1, \ldots, I,$$

where X_{in} is the observed value for the n-th individual in the i-th source population. Thus, the first terms in both numerator and denomerator of equation (7b) represent the known (unambiguous) individuals from the i-th population, simply added to the corresponding (ambiguous) terms of equation (7a) for the mixed harvest. The iterative sequence thus becomes equation (4) → (5) → (6) → (7b) → (5) → (6) → (7b) → (5) → . . ., and so on. This treatment is intermediate between that for the case of no source population data, where the source frequencies must be estimated completely from the harvest, and that for the case encompassed by the standard GSI algorithm, where the source population frequencies are assumed to be precisely those of the baseline sample. The importance of this change is that the source population data influence the allele frequency estimates throughout, but they do not completely determine those estimates. With large enough source population samples, the impact of the harvest on the source population allele frequencies will be trivial, but as we have already mentioned and as we shall see later, routine practice does not yield large sample sizes for the source populations.

The data set from the source populations and the harvest is frequently incomplete. Some electrophoretic gels are unreadable, in whole or in part; some individuals do not produce clear banding patterns for all enzyme systems; enzyme systems are added to and subtracted from the assay battery over time. The net result is a large data base with numerous holes' (missing data). The usual GSI treatment groups all individuals with a particular set of loci assay into a single block; thus, the data are broken up into nonoverlapping blocks which are complete internally. The GSI analysis optimizes all blocks simultane-

ously, a straight forward but cumbersome extension of equation (2a) to (11).

To capitalize on all of the available data, we have devised an alternative procedure that is a simple extension of our iterative estimation scheme in the absence of source population data. We provide a dummy X-vector for each missing locus, initially replacing the allelic count vectors of equation (8a) with the vector of their expectations for the k-th locus, i.e. with a vector of the allele frequencies at that locus:

$$(8b) \quad X'_{ik} = [p_{i1}^{(0)}, p_{i2}^{(0)}, p_{i3}^{(0)}]$$

for a missing genotype in the i-th source population, and with:

$$(8c) \quad X'_{hk} = [\Sigma_i m_i p_{i1}^{(0)}, \Sigma_i m_i p_{i2}^{(0)}, \Sigma_i m_i p_{i3}^{(0)}]$$

for a missing genotype in the harvest. After each iteration, the new estimates of the p_{ij}'s and the m_i's are inserted into equation (8a) and (8b), giving the overall iterative sequence of equation (4) → (5) → (6) → (8) → (7b) → (4) →. . ., and so on. Thus, we update the 'holes' as we go along, so that we can treat the total data set as though it had no holes. The procedure is designed to yield unbiased estimates of all the parameters for any model under consideration. We need merely remember that the likelihood for a missing locus is unity for any model, so that the missing values do not influence the choice of model.

We next turn to formal hypothesis testing, which is a bit more elaborate than for the situation where there are no source population data. The various H_i are not submodels of each other, and cannot be formally compared by χ^2 analysis. Clearly, however, that H_i with the highest likelihood is the most compatible with the data, and those with substantially smaller likelihoods can plausibly be ruled out of contention. Each of the models H_i (with $m_i = 1$ and all other m's $= 0$) is a special case (submodel) of the model H_I (all m_i's ≥ 0), and each H_i can be formally tested against H_I. To test H_i against H_I, we substitute the appropriate estimated values of the m_i's and p_{ij}'s into equation (12a) and (12b), and then compute:

$$(15) \quad \Lambda_{i,I} = 2\,[\log L(H_I \mid \text{data}) - \log L(H_i \mid \text{data})],$$

which is χ^2-distributed with $(I - 1)$ degrees of freedom.

As with equation (10), it is possible to consider a number of intermediate hypotheses, where the harvest is considered to be a mixture of some subset of the source populations. Because there are different pairs of populations that could be the relevant source populations, many trios, and so on, there are many different analogues of equation (11). Any sequence of models chosen so that each element is embedded within the next most inclusive model forms a proper testing cascade; other sequences are not proper cascades. For example:

H_1: harvest is a sample from source population 1 only,
H_{13}: harvest is a sample from source populations 1 and 3 only,
H_{123}: harvest is a sample from source populations 1, 2 and 3 only,
H_I: harvest is a sample from all I source populations,

is a legitimate testing cascade, yielding:

$$(16a) \quad \Lambda_{1,I} = \Lambda_{1,13} + \Lambda_{13,123} + \Lambda_{123,I},$$

where the four test criteria are χ^2-distributed with $(I - 1)$, 1, 1, and $(I - 3)$ degrees of freedom, respectively. If desirable, $\Lambda_{123,I}$ can be further partitioned into $(I - 3)$ single degree of freedom components. There are no set rules for choosing the proper sequence, but the general strategy is a step-wise exploration of possibilities. One chooses the best single source population to combine with the harvest, then finds the best additional source, and so on. For even a modest number of potential sources, exhaustive enumeration is not possible, but our experience has been that the best cascade generally emerges rather clearly from a little sequential model fitting.

Even a model specifying that all I populations contribute to the mix will seldom provide a perfect fit to the data, and it is well worth considering the hypothesis that there are additional sources (not sampled) that contribute to the mix. It is possible to add sequential components to equation (16a) for these extra populations, much as was done for equation (11):

$$(16b) \quad \Lambda_{i,I+k} = \Lambda_{i,I} + \Lambda_{I,I+1} + \Lambda_{I+1,I+2} + \ldots + \Lambda_{I+k-1,I+k},$$

For each additional source invoked, it is necessary to estimate J additional allele frequency parameters and one additional mixture parameter, so that each component of the sequential decomposition must be compared with a χ^2 with $(J + 1)$ degrees of freedom. Only large increases in Λ will be meaningful or significant, since we must estimate a whole battery of extra allele frequency parameters from the mixed harvest itself. It is important to assess the possibility that we have overlooked a major contributing source population. As we will show later, we can hope to detect the effect of major unsampled stocks, but there is little hope of detecting minor contributors.

Bonneville Egg Bank Study

Populations Sampled

Our study involves fall-run chinook salmon (i.e. those stocks that enter freshwater in the fall) from the mid-to-upper Columbia River Basin (Fig. 1). Fall-run chinook salmon in this area of the river occur as two morphological types; 'tules and 'upriver brights.' Tules are dark (sexually mature) fish, returning primarily to hatcheries in the low-to-mid portions of the Columbia River. Upriver brights are silvery fish that may have a considerable distance to travel before reaching their spawning grounds. Because these upriver brights have not completed the massive physiological transformation associated with spawning, their flesh is highly prized, and they represent a highly marketable resource. Interceptions are routinely made at Bonneville Dam for an egg bank program, the goal of which is to increase the upriver bright portion of fall-run chinook salmon. Knowledge of the genetic makeup of egg bank contributors is necessary, because tules and brights cannot always be distinguished morphologically. It is also important to ensure that interceptions do not substantially reduce the already depleted wild stocks from the Snake River, stocks that still have the farthest distance to traverse and the greatest hazards to survive before reaching their natural spawning areas.

Samples of returning fish were intercepted at Bonneville Dam in 1980 ($N = 1179$) and 1981 ($N = 475$) for an egg bank program. Baseline data (558 fish) were collected in 1981 and 1982 from seven potential source populations. Spring Creek Hatchery [SC], just below Bonneville Dam, is the major contributor to the tule run, and allele frequencies for this stock are representative of those for other potentially contributing tule stocks (Milner et al. 1985). Upriver bright stocks were sampled in the middle Columbia region (Deschutes River [DR]), upper Columbia region (White Bluffs [WB], Vernita Bar [VB], and Priest Rapids [PR]), and at the Ice Harbor dam on the lower Snake River, from which samples were taken to hatcheries at Tucannon [TU] and Dworshak [DW].

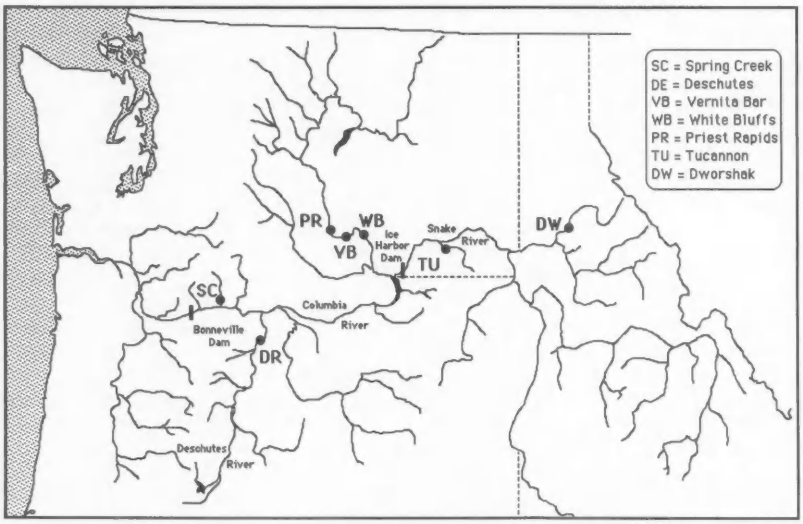

FIG. 1. Map of the source localities relevant to the Bonneville egg bank collections of 1980 and 1981.

Estimates of the respective contributions of these stocks to the 1980 and 1981 Bonneville egg bank catches have been computed with the current GSI model, treating the baseline allele frequencies as known without error (Milner et al. 1985). In those analyses, the three upper Columbia samples (WB, VB, PR), all from the Hanford Reach area, were pooled into a single 'source,' because their allele frequencies were comparable. Similarly, the two Ice Harbor Dam samples (TU, DW) were pooled, as they were taken at the same locality on different days. A χ^2-heterogeneity analysis for all twelve loci provides no compelling evidence of genetic divergence between WB and VB ($\chi_{18}^2 = 15.29$, $0.50<P<0.70$), but PR is different from WB and VB together ($\chi_{18}^2 = 29.37$, $0.02<P<0.05$). We will here examine the consequences of pooling all three Upper Columbia gene pools, as opposed to pooling only WB and VB. The two Ice Harbor Dam samples are not quite heterogeneous ($\chi_{18}^2 = 23.79$, $0.10<P<0.20$), although it would not be surprising if the genetic composition of fish intercepted at Ice Harbor on different days should vary; there are a number of Snake River stocks that must pass this dam. We keep these two stocks separate for analytical purposes.

Collection and Assay Procedures

Tissue samples (skeletal muscle, liver, heart, eye) from individual fish were collected in the field, frozen on dry ice, and shipped to the National Marine Fisheries Service laboratory at Manchester, Washington. Procedures for protein extraction and starch gel electrophoresis generally followed those described by Aebersold et al. (1987). Over 100 loci have been screened for the coast-wide chinook salmon data base and more than 25 have been found to be polymorphic (Utter et al. 1989). A smaller number of loci exhibit variability that is informative for our geographically more restricted set of populations. Table 1 lists the allelic counts for all source populations and the egg bank harvests for 12 codominant, polymorphic loci (*AH4, DPEP1, GR, HAGH, IDH3, LDH5, MDH3, MPI, PEP-LT, PGK2, SOD1, TAPEP1*) used in the analysis reported here. Sample sizes vary somewhat from locus to locus, because some individuals do not yield reliable typing for particular loci. In addition, the *GR, HAGH, PEP-LT*, and *PGK2* loci were not added to the assay battery until after the 1980 harvest, reducing the analysis of the 1980 collection to an eight-locus problem.

Interpretation of genetic variation at the *IDH* and *MDH* systems is complicated because these are pairs of duplicated loci (isoloci) that cannot be distinguished electrophoretically (Allendorf and Thorgaard 1984). Individual genotypes are ambiguous for isoloci, because more than one two-locus genotype can express the same phenotype. For current GSI analyses, both loci of an isolocus pair are presumed to have the same allele frequencies (the average over both loci), and those average frequencies are used to calculate the likelihood of observing the distribution of phenotypes in the mixture. This approach is satisfactory if frequencies at the two loci actually are similar but leads to bias if they are not. An alternative is to assume that all variation is due to just one locus of the pair, the other locus being monomorphic. This assumption is attractive, because it allows genotypes to be scored unambiguously, but it is tenable only if no individuals have more than two doses of the variant allele(s).

In the seven baselines comprising the Bonneville Egg Bank Study, only one individual (of 558) was scored for three 'doses' of the variant *IDH-3,4* allele, and no individuals with three doses of the variant *MDH-3,4* allele were found. Thus, although it is apparent that both *IDH* loci must be variable in at least some populations, the frequency of these variants appears to be small enough at the second locus that attributing all variation to one locus is more nearly correct than assigning both loci identical (and intermediate) frequencies. Moreover, Waples (1988) has shown that if both loci are variable, but genotypes are scored on the assumption that only one locus is segregating, a standard test of Hardy-Weinberg equilibrium will (on average) indicate a deficiency of heterozygotes. In the Bonneville egg bank study, six of the seven baselines have small but nonsignificant heterozygote excesses for both *IDH-3,4* and *MDH-3,4*. There is thus no evidence for recurring heterozygote deficien-

TABLE 1. Allelic counts for 12 polymorphic enzyme systems in each of seven source populations and two harvests of the Bonneville egg bank study.

Locus and Allele	Bonneville Dam		Source population (baseline) samples						
	1980	1981	[SC]	[DR]	[WB]	[VB]	[PR]	[TU]	[DW]
Aconitate hydratase [E.C. (4.2.1.3): *AH4*]									
AH4-1	1648	768	99	85	69	187	160	179	169
AH4-2	362	168	1	10	15	39	34	17	27
AH4-3	6	3	0	3	0	0	0	0	1
AH4-4	0	1	0	0	0	0	0	2	3
Glycly-leucine peptidase [E.C. (3.4.13.11): *DPEP1*]									
DPEP1-1	2295	919	98	88	74	224	197	192	191
DPEP1-2	63	27	2	10	6	2	1	6	7
Isocitrate dehydrogenase [E.C. (1.1.1.42): *IDH3*]									
IDH3-1	2019	802	99	92	71	196	164	152	186
IDH3-2	297	141	1	6	17	34	35	10	6
IDH3-3	10	3	0	0	0	0	1	0	0
Lactate dehydrogenase [E.C. (1.1.1.27): *LDH5*]									
LDH5-1	2107	848	100	98	82	216	189	196	192
LDH5-2	27	14	0	0	2	4	3	0	1
LDH5-3	0	0	0	0	0	4	0	1	
Malate dehydrogenase [E.C. (1.1.1.37): *MDH3*]									
MDH3-1	2224	897	93	95	80	216	182	194	186
MDH3-2	74	29	7	2	4	10	12	2	2
MDH3-3	54	22	0	1	0	4	6	4	4
Mannose-6-phosphate isomerase [E.C. (5.3.1.8.): *MPI*]									
MPI-1	1620	671	57	69	61	155	141	160	154
MPI-2	719	269	36	29	25	75	59	38	44
MPI-3	15	6	7	0	0	0	0	0	0
Superoxide dismutase [E.C. (1.15.1.1): *SOD1*]									
SOD1-1	1264	516	53	72	43	115	110	146	136
SOD1-2	1090	430	47	26	43	113	90	54	64
SOD1-3	2	0	0	0	0	0	0	0	0
Leucylglycyl-glycine peptidase [E.C. (3.4.11.4): *TAPEP1*]									
TAPEP1-1	1884	778	78	92	69	176	157	184	172
TAPEP1-2	470	172	22	6	19	48	41	10	22
Glutathione reductase [E.C. (1.6.4.2): *GR*]									
GR-1	*	910	63	93	88	226	195	100	200
GR-2	*	18	37	5	0	0	5	0	0
Hydroxyacylglutathione hydrolase [E.C. (3.1.2.6): *HAGH*]									
HAGH-1	*	621	92	91	80	213	200	67	198
HAGH-2	*	3	8	1	0	1	0	3	2
Leucyl-tyrosine peptidase [E.C. (3.4.11.-): *PEP-LT*]									
PEP-LT-1	*	737	100	88	71	177	102	190	164
PEP-LT-2	*	203	0	10	15	41	28	10	20
Phosphoglycerate kinase [E.C. (2.7.2.3): *PGK2*]									
PGK2-1	*	584	86	62	57	124	126	103	113
PGK2-2	*	18	14	36	29	92	70	93	85
Maximum sample size	2358	950	100	98	88	230	200	200	200

*No data available.

cies, as would be expected if both loci contained variant alleles at appreciable frequency. As a consequence, we arbitrarily assign the polymorphisms to *IDH-3* and *MDH-3*, respectively, and ignore *IDH-4* and *MDH-4* as essentially monomorphic. The likelihood procedures developed here could be generalized for any sort of scoring ambiguities one might encounter in practice (see Waples 1988), but in the absence of any real need to do so here, we will avoid those complications.

Validating the Algorithm

Before examining the actual 1980 and 1981 egg bank collections, we need to establish that the estimation and testing algorithm developed above performs as advertized. A number of previous simulation studies have shown that the standard GSI algorithm provides accurate and precise stock composition estimates (m_i's), as long as the usual assumptions are met (Milner

et al. 1981; Fournier et al. 1984; Beacham et al. 1985; Millar 1987; Wood et al. 1987; Pella and Milner 1987). An elaborate analysis of a large additional series of simulated mixtures would be excessive here. Our new developments are designed to deal with a pair of limitations commonly encountered in practice: (i) the inability to specify all possible source populations, and (ii) the necessity of dealing with small samples of those sources that can be specified. A few illustrations will show that the algorithm performs as advertised under most circumstances, and that it encounters trouble in predictable circumstances.

We present in Table 2 the analytical outcomes for three contrived situations. The first of these involves contrived mixtures of two genetically disparate source populations [SC and DW] — where resolution should be simple. We drew five different mixtures from these two source populations, in the following fashion. We first defined seven gene pools having parametric allele frequencies to match those observed in our samples from the seven source populations. We then established 12-locus Hardy-Weinberg frequencies for each of the gene pools separately. We drew 100 individuals from each gene pool to obtain a baseline sample; these stock 'samples' are all genetically similar to those actually observed, but they are not identical.

We next draw a random number from a uniform distribution, U(0,1), and if it was less than 0.10, we drew a random genotype from the [SC] genotype array; otherwise, we drew a random genotype from the [DW] array. We drew 500 random fish in this fashion to construct a sample from the mixed harvest, whose observed composition was 12.4% [SC] and 87.6% [DW] in our mixed harvest sample. [Whatever the true mixture fractions in the harvest population, we draw only a sample for analysis.] We conducted analyses of the mixture and source populations, and the results are shown as the first set of entries in Table 2a. In similar fashion, we drew sample collections of [SC] and [DW] from parametric 30:70, 50:50, 70:30, and 90:10 mixtures, and the results are shown in Table 2a.

A perusal of the results shows two points. First, the estimated mixture fractions are close to the parametric values for these genetically disparate source populations when only those two sources are included in the model, and the mixed model yields a large improvement in log-likelihood over models of either single component. Second, the complete model — with all seven sources, shows negligible contributions from those sources not actually contributing, and the differences in log-likelihood that emerge from fitting an extra five parameters are unconvincing. The allele frequency estimates (not shown) for the two fitted sources differ only in the second decimal place from those of the source collection samples themselves. These results are reassuring.

The second situation involves mixtures of two very similar source populations [TU and DW] — where resolution could well be problematic. We set these contrived mixtures up in the same fashion as for those in Table 2a, again as samples from mixed harvests with parametric proportions of 10:90, 30:70, 50:50, 70:30, and 90:10 (Table 2b). There is not much genetic difference between [TU] and [DW], and there is a wider departure between estimated and expected mixture fractions than was the case in Table 2a, where the contributing sources were quite different. In addition, the improvements in log-likelihood over the best of the single source models are miniscule except for the 50:50 mix. However, the other five sources (full model) contribute nothing, and there is no reason to invoke an out-population. The allele frequency estimates differ no more from those of the source population samples (second decimal place) than these do from each other. Since the source of the ambiguity is that these latter are so similar, we obtain reasonable source population allele frequency estimates. Although it will be difficult to separate the relative contributions of a set of genetically very similar source populations, their collective contribution is well estimated. With genetically homogeneous source populations, that is about all we can ask.

The third situation involves mixtures of three components [SC, DR, and TU] with only two of the relevant sources sampled [SC and DR]. Here, the question is how well we can detect the unsampled outpopulation [OP = TU] when it really has contributed. The contrived mixture samples were constructed in the same fashion as those above, fish drawn from mixtures of [SC], [DR], and [TU] with parametric proportions of 495:495:10, 45:45:10, 35:35:30, 25:25:20, and 5:5:90. The numerical results are presented in Table 2c. Ignoring the possibility of an unsampled out-population, we discover that the resulting estimates of m_1 and m_2 are biased, and that the size of the bias increases with the contribution of the unsampled source population. In this case, [DR] is more similar to [TU] than is [SC], and [DR] thus (falsely) receives the out-population's share of the credit for the mixture, with corresponding biases in the allele frequency estimates. If we allow for the unsampled out-population [TU], the estimates of the m-values for the sampled populations fall more in line with their real contributions, although in this case, the contribution of [DR] is underestimated a bit, most of the difference being attributed to the out-population. The allele frequency estimates become closer to those of the sampled source populations (usually second decimal place differences only), but those for the unsampled out-population are somewhat more erratic. Large changes in the m-values upon addition of an unsampled out-population, accompanied by substantial changes in the log-likelihood, are an indication of a hidden contributor. The differences in log-likelihood ($H_{1,2}$ versus $H_{1,2,8}$) increase with the size of the contribution of the unsampled out-population. Only when the contribution of the out-population becomes large does the log-likelihood for H_8 exceed that for $H_{1,2}$, and as it becomes predominant, the log-likelihood for H_8 is almost as large as that for $H_{1,2,8}$, suggesting that the mixture is a single (unsampled) source population. The test for the unsampled out-population behaves well, but the allele freqency estimates are subject to larger biases than is the case for sampled populations. We can do a better job of detecting the unsampled out-population than we can of characterizing it. The only good way to characterize the out-population would be to obtain samples from it by additional geographic sampling. Our analysis behaves as advertised.

1980 Harvest

Our approach to resolving the 1980 harvest from the Bonneville Dam Egg Bank Collection into one or more of the seven sampled baselines is depicted in the various models of Table 3, the most informative subset from a very large number of trials involving many different combinations of sources. For the case at hand, a simple testing cascade seems to tell the story very well. We begin the testing cascade with H_4 [VB]; this is the most likely single-source model, but there is little resolution between this 'best' single-source model and H_3 [WB]. We noted earlier that there is little evidence for heterogeneity between WB and VB, so this result was expected. Adding Deschutes River [DR] to form H_{24}, we achieve a substantial improvement over H_4 ($\chi_1^2 = 9.22$). The point of diminishing returns comes

TABLE 2. Estimated m-values and log-likelihoods for simulated mixtures of populations from the Bonneville Dam egg bank study: (a) mixtures of Spring Creek [SC = 1] and Dworshak [DW = 7], (b) mixtures of Tucannon [TU = 6] and Dworshak [DW = 7], (c) mixtures of Spring Creek [SC = 1], Deschutes River [DR = 2], and Tucannon [TU = 6], with Tucannon treated as an unsampled out-population [OP = 8]; samples sizes are $N = 100$ for each baseline and $N = 500$ for the mixed harvest.

Sample mixture fraction	Model	Estimated mixture fractions								Df	$-\log L$
		[SC]	[DR]	[WB]	[VB]	[PR]	[TU]	[DW]	[OP]		
a.	H_1	1.000	*	*	*	*	*	*	*	119	7529.79
$m_1 = 0.124$	H_7	*	*	*	*	*	*	1.000	*	119	7318.56
$m_7 = 0.876$	$H_{1,7}$	0.101	*	*	*	*	*	0.899	*	120	7252.08
	H_{1-7}	0.101	0.000	0.015	0.000	0.000	0.000	0.884	*	125	7251.84
	H_1	1.000	*	*	*	*	*	*	*	119	7645.29
$m_1 = 0.310$	H_7	*	*	*	*	*	*	1.000	*	119	7560.39
$m_7 = 0.690$	$H_{1,7}$	0.285	*	*	*	*	*	0.715	*	120	7396.38
	H_{1-7}	0.284	0.001	0.014	0.001	0.000	0.000	0.700	*	125	7396.13
	H_1	1.000	*	*	*	*	*	*	*	119	7659.44
$m_1 = 0.490$	H_7	*	*	*	*	*	*	1.000	*	119	7653.89
$m_7 = 0.510$	$H_{1,7}$	0.457	*	*	*	*	*	0.543	*	120	7446.12
	H_{1-7}	0.453	0.029	0.021	0.004	0.000	0.000	0.492		125	7444.67
	H_1	1.000	*	*	*	*	*	*	*	112	7581.21
$m_1 = 0.692$	H_7	*	*	*	*	*	*	1.000	*	112	7660.55
$m_7 = 0.308$	$H_{1,7}$	0.665	*	*	*	*	*	0.335	*	113	7425.64
	H_{1-7}	0.665	0.000	0.002	0.005	0.000	0.000	0.327	*	125	7425.46
	H_1	1.000	*	*	*	*	*	*	*	112	7405.85
$m_1 = 0.902$	H_7	*	*	*	*	*	*	1.000	*	112	7585.75
$m_7 = 0.098$	$H_{1,7}$	0.891	*	*	*	*	*	0.109	*	113	7345.06
	H_{1-7}	0.893	0.000	0.008	0.000	0.000	0.024	0.075	*	125	7343.79
b.	H_6	*	*	*	*	*	1.000	*	*	119	7201.47
$m_6 = 0.108$	H_7	*	*	*	*	*	*	1.000	*	119	7184.79
$m_7 = 0.892$	$H_{6,7}$	*	*	*	*	*	0.098	0.902	*	120	7183.87
	H_{1-7}	0.000	0.000	0.000	0.000	0.000	0.095	0.905	*	125	7183.87
	H_6	*	*	*	*	*	1.000	*	*	119	7171.76
$m_6 = 0.274$	H_7	*	*	*	*	*	*	1.000	*	119	7162.07
$m_7 = 0.726$	$H_{6,7}$	*	*	*	*	*	0.196	0.804	*	120	7160.18
	H_{1-7}	0.000	0.000	0.000	0.000	0.000	0.194	0.806	*	125	7160.18
	H_6	*	*	*	*	*	1.000	*	*	119	7093.93
$m_6 = 0.508$	H_7	*	*	*	*	*	*	1.000	*	119	7092.06
$m_7 = 0.492$	$H_{6,7}$	*	*	*	*	*	0.387	0.613	*	120	7088.60
	H_{1-7}	0.000	0.000	0.000	0.000	0.000	0.386	0.614	*	125	7088.60
	H_6	*	*	*	*	*	1.000	*	*	119	7008.83
$m_6 = 0.710$	H_7	*	*	*	*	*	*	1.000	*	119	7015.51
$m_7 = 0.290$	$H_{6,7}$	*	*	*	*	*	0.833	0.167	*	120	7008.83
	H_{1-7}	0.000	0.000	0.000	0.000	0.000	0.823	0.176	*	125	7008.83
	H_6	*	*	*	*	*	1.000	*	*	119	6955.14
$m_6 = 0.912$	H_7	*	*	*	*	*	*	1.000	*	119	6969.05
$m_7 = 0.088$	$H_{6,7}$	*	*	*	*	*	0.972	0.028	*	120	6955.14
	H_{1-7}	0.000	0.000	0.000	0.000	0.000	0.968	0.031	*	125	6955.14
c.	H_1	1.000	*	*	*	*	*	*	*	102	7269.85
$m_1 = 0.498$	H_2	*	1.000	*	*	*	*	*	*	102	7272.72
$m_2 = 0.490$	H_8	*	*	*	*	*	*	*	1.000	119	7209.22
$m_8 = 0.012$	$H_{1,2}$	0.512	0.488	*	*	*	*	*	*	103	7125.34
	$H_{1,2,8}$	0.513	0.471	*	*	*	*	*	0.016	121	7113.19
	H_1	1.000	*	*	*	*	*	*	*	102	7260.90
$m_1 = 0.442$	H_2	*	1.000	*	*	*	*	*	*	102	7243.36
$m_2 = 0.462$	H_8	*	*	*	*	*	*	*	1.000	119	7188.92
$m_8 = 0.096$	$H_{1,2}$	0.455	0.545	*	*	*	*	*	*	103	7094.02
	$H_{1,2,8}$	0.462	0.324	*	*	*	*	*	0.214	121	7080.47
	H_1	1.000	*	*	*	*	*	*	*	102	7174.01
$m_1 = 0.328$	H_2	*	1.000	*	*	*	*	*	*	102	7118.20
$m_2 = 0.366$	H_8	*	*	*	*	*	*	*	1.000	119	7074.80
$m_8 = 0.306$	$H_{1,2}$	0.328	0.672	*	*	*	*	*	*	103	6993.69
	$H_{1,2,8}$	0.337	0.262	*	*	*	*	*	0.401	121	6966.18

TABLE 2. (*continued*)

	H_1	1.000	*	*	*	*	*	*	*	102	7083.87
$m_1 = 0.230$	H_2	*	1.000	*	*	*	*	*	*	102	6987.45
$m_2 = 0.268$	H_8	*	*	*	*	*	*	*	1.000	119	6948.99
$m_8 = 0.502$	$H_{1,2}$	0.231	0.769	*	*	*	*	*	*	103	6884.12
	$H_{1,2,8}$	0.246	0.187	*	*	*	*	*	0.567	121	6848.47
	H_1	1.000	*	*	*	*	*	*	*	102	6784.45
$m_1 = 0.046$	H_2	*	1.000	*	*	*	*	*	*	102	6590.61
$m_2 = 0.044$	H_8	*	*	*	*	*	*	*	1.000	119	6537.48
$m_8 = 0.910$	$H_{1,2}$	0.032	0.968	*	*	*	*	*	*	103	6566.26
	$H_{1,2,8}$	0.040	0.035	*	*	*	*	*	0.925	121	6533.74

*Sources not considered for the model in question.

rapidly, however; adding a third component source population [WB] to the mixture (H_{234}) leads to no real improvement ($\chi_1^2 = 2.88$) over the previous model H_{24}. As seen from Table 3, there is nothing to be gained from adding further source populations to the harvest, and our most parsimonious model for the seven sampled baselines is H_{24}. In addition, a regular pattern emerges from Table 3 for all models with a combination of two or more sources. Two of the three source populations from the Upper Columbia region account for roughly 88% of the harvest, with Deschutes River [DR] accounting for the remaining 12% of the harvest.

We may also add a single unsampled 'out-population' [OP] to the harvest, either as the sole source ($H_8 = H_h$), or as one of several contributors. The addition of [OP] to the collection of source populations changes the starting point of the analysis but not the strategy. The starting point is ($H_8 = H_h$). Mixtures of the best combinations without an outlier are added to [OP] until the point of no significant improvement is reached. This point is H_{238}, since the next most inclusive model, H_{2348}, is not a compelling improvement ($\chi_1^2 = 2.48$). When adding sampled baselines to [OP], the analysis tends to apportion about 65% of the harvest to the Upper Columbia region (either WB or VB or both), 12% to Deschutes River [DR], and the rest to [OP]. Again, there is not much resolution among the various models, and we note that Priest Rapids, part of the Upper Columbia collection, does not make a meaningful contribution to any of them. We also note that neither the tules from Spring Creek [SC] nor the upriver brights from above Ice Harbor Dam [TU or DW] make a significant contribution in any of the models, including models lacking an out-population.

We should mention here that while both H_f and H_8 are proper submodels of H_{f8}, neither is a proper submodel of the other. Thus, the difference in log-likelihoods between the best model lacking an out-population (H_{24}) and the best model with an out-population (H_{238}) is not a valid χ^2-test. Nevertheless, since the difference between them is very small, and since H_{24} is almost as good as H_8, while requiring 14 fewer parameters, there is little to be gained by invoking [OP], the unsampled out-population.

1981 Harvest

Similar analysis of the 1981 harvest (Table 3) shows [WB] as the best single-source model, rather than [VB], but there is again very little to choose between them; indeed, even [PR] gives about the same fit. Adding [DR] to [WB] results in an improvement in the model ($\Lambda_{3,23} = 4.58 \sim \chi_1^2$). The addition of [VB] as a third source population yields a negligible improvement ($\Lambda_{23,234} = 0.00 \sim \chi_1^2$). Although there is no compelling reason to fit another source population, we note that [PR] has a nontrivial m-value if it is added (H_{2345}). The fact that the m-values of the Upper Columbia sources change so drastically from model to model, with trivial changes in the log-likelihood, is an indication that the outcome is sensitive to small differences in allele frequencies of these source populations, another way of saying that the likelihood function is very flat. Leaving aside, for the moment, the question of the optimal apportionment of mixture fractions among them, it is clear that the Upper Columbia sources contribute about 90% of the harvest, with [DR] contributing the remaining 10%.

The addition of an unsampled out-population [OP] to the analysis yields a parsimonious model of H_{248} [DR + VB + OP]. Examination of the various models in Table 3 again shows, however, the sensitivity of the composition fractions within the Upper Columbia set to small allele frequency differences among these source populations. With [OP], we see that [VB] is the Upper Columbia source of choice, rather than [WB], and combinations of [OP], [DR], [WB], and [VB], with or without [PR], yield erratic m-values from model to model, a sure sign of limited resolution. Ignoring the ambiguity within the Upper Columbia set, about 77% of the harvest consists of Upper Columbia fish, with [DR] providing 12%, and [OP] providing the rest. Again, neither the tules from Spring Creek [SC] nor the upriver brights from as far upriver as Ice Harbor Dam [TU and DW] make a significant contribution. The results are similar to those from 1980.

Considering the difficulty of distinguishing among the three Upper Columbia sources, it is reasonable to ask whether it is worthwhile to pool those sources into a single Hanford Reach [HR] set, or at least to pool [WB] and [VB], leaving [PR] separate. The same question arises with regard to the two Ice Harbor Dam samples, [TU] and [DW]. Recall that for our earlier validation efforts, we showed that [TU] and [DW] were so similar that precise estimatation of their relative mixture contributions were difficult. The outcome of the egg bank analysis is reminiscent of the contrived examples with [TU] and [DW]. Careful analysis of the 1980 and 1981 egg bank collections shows that since neither [TU] nor [DW] contribute to these harvests, the decision of whether or not to pool them makes no real difference to the outcome. The results for the Hanford Reach collections are more complicated, but the salient features are captured in Table 4, where we present the m-values for various combinations of [DR], [WB], [VB], [PR], and [OP]. In the absence of an out-population, the results are virtually identical for both years if we pool all three Upper Columbia sources ($H_{2(345)}$) or just the [WB] and [VB] sources ($H_{2(34)5}$); 88–89% of the egg bank collection comes from the [WB] and/or [VB], the rest being from [DR]; [PR] does not contribute

TABLE 3. Estimated mixture fractions and log-likelihoods for several mixture models for the 1980 and 1981 harvests of the Bonneville Dam Egg Bank Study; sample sizes for source populations and egg bank harvests are presented in Table 1.

Mixture model	Year	Estimated mixture fractions								(1980)		(1981)	
		[SC]	[DR]	[WB]	[VB]	[PR]	[TU]	[DW]	[OP]	Df	$-\log L$	Df	$-\log L$
H_1		1.000	*	*	*	*	*	*	*	105	8255.29	126	6826.59
H_2		*	1.000	*	*	*	*	*	*	105	8245.42	126	6712.03
H_3		*	*	1.000	*	*	*	*	*	105	8221.09	126	6686.43
H_4		*	*	*	1.000	*	*	*	*	105	8220.13	126	6689.35
H_5		*	*	*	*	1.000	*	*	*	105	8231.77	126	6692.47
H_6		*	*	*	*	*	1.000	*	*	105	8272.66	126	6751.81
H_7		*	*	*	*	*	*	1.000	*	105	8255.49	126	6721.89
H_{23}	(1980)	*	0.100	0.900	*	*	*	*	*	106	8218.79	—	—
	(1981)	*	0.099	0.901	*	*	*	*	*	—	—	127	6684.14
H_{24}	(1980)	*	0.120	*	0.880	*	*	*	*	106	8215.52	—	—
	(1981)	*	0.106	*	0.894	*	*	*	*	—	—	127	6684.96
H_{234}	(1980)	*	0.120	0.224	0.656	*	*	*	*	107	8214.08	—	—
	(1981)	*	0.097	0.903	0.000	*	*	*	*	—	—	128	6684.14
H_{2345}	(1980)	*	0.120	0.213	0.667	0.000	*	*	*	108	8214.08	—	—
	(1981)	*	0.110	0.361	0.181	0.348	*	*	*	—	—	129	6683.84
H_1	(1980)	0.010	0.119	0.210	0.661	0.000	0.000	0.000	*	111	8214.08	—	—
	(1981)	0.022	0.052	0.363	0.185	0.347	0.026	0.005	*	—	—	132	6681.44
$H_8 = H_h$		*	*	*	*	*	*		1.000	120	8213.29	144	6677.06
H_{238}	(1980)	*	0.109	0.430	*	*	*	*	0.461	122	8206.58	—	—
	(1981)	*	0.078	0.302	*	*	*	*	0.620	—	—	146	6674.81
H_{248}	(1980)	*	0.121	*	0.636	*	*	*	0.243	122	8206.69	—	—
	(1981)	*	0.124	*	0.772	*	*	*	0.104	—	—	146	6672.26
H_{2348}	(1980)	*	0.123	0.245	0.426	*	*	*	0.206	123	8205.45	—	—
	(1981)	*	0.124	0.000	0.772	*	*	*	0.104	—	—	147	6672.25
H_{23458}	(1980)		0.123	0.245	0.426	0.000	*	*	0.206	124	8205.45	—	—
	(1981)		0.123	0.003	0.770	0.000	*	*	0.104	—	—	148	6672.25
H_{18}	(1980)	0.009	0.122	0.240	0.422	0.000	0.000	0.000	0.207	127	8205.45	—	—
	(1981)	0.022	0.083	0.005	0.790	0.000	0.001	0.000	0.099	—	—	151	6669.96
GSI	(1980)	0.07	0.06	[—	0.79	—]	[—	0.08	—]	Milner et al. (1985) results			
	(1981)	0.02	0.06	[—	0.86	—]	[—	0.07	—]				

*Source not included in the model in question.

meaningfully to either egg bank collection. The consistency of these results stands in marked contrast to those from treating the Upper Columbia sources separately (e.g. H_{2345} and its various submodels), where the m-coefficients are quite sensitive to model choice. The results of adding an out-population [OP] are even more revealing. Here, pooling [PR] with [WB] and [VB] leads to instability of the m-values across both years and models. Evidently, pooling is useful, but should be restricted to very similar source populations.

The fact that the 1980 and 1981 egg bank collections show such consistency of composition, not an inherent feature of the analysis, is an interesting (but perhaps not surprising) result. The two collections were made at roughly the same time of year (25 August–18 September 1980 and 24 August–8 October 1981). Whether Bonneville Dam collections at other seasons would yield higher proportions of other sources remains to be seen, but at least for the collections in hand, the management objective of enriching the catch for upriver Columbia brights has been met, without making inroads among fish destined for the Snake River spawning grounds.

Discussion

The important results from the analysis of the egg bank collections can be summarized as follows: (1) In neither year is it necessary to postulate a contribution by all of the potential source populations to the mixure; both mixtures can be adequately described as comprised of fish from the Upper Columbia [WB and VB] region and Deschutes River [DR]. (2) A slightly better fit (as will inevitably be the case if more parameters are used) is obtained if an (unsampled) out-population is invoked, but the resulting increase in log L for both 1980 and 1981 is small relative to the increase in degrees of freedom entailed in estimating additional parameters. There is no compelling evidence that any unsampled stocks contribute significantly to the mix. (3) The Upper Columbia samples, [WB] and [VB], and to a lesser extent [PR], are so similar genetically that there is little hope of precisely estimating their relative contributions. It is useful to examine the first two points in relation to composition estimates obtained using the current GSI algorithm; the third point is discussed later.

In their analysis of the 1980 and 1981 mixtures, Milner et al. (1985) considered four source populations: [SC], [DR], Hanford Reach [WB + VB + PR], and the Snake River [TU + DW]. Comparison of their results (final entries of Table 3) with those of the present analysis indicates one major point of agreement; in both years, the majority of the collection (79–90%) is assigned to the Hanford Reach stocks. Thus, it is clear that the primary goal of using upriver bright stocks from the Hanford Reach area of the Upper Columbia River for the egg

TABLE 4. Estimated mixture fractions for the most parsimonious pooled and unpooled models for the 1980 and 1981 harvests of the Bonneville Dam egg bank study. Results in brackets are for source populations that have been pooled prior to analysis.

Mixture model	Year	Mixture fractions [DR=2]	[WB=3]	[VB=4]	[PR=5]	[OP=8]
No out-population						
$H_{2(345)}$	(1980)	0.121	[.....	0.879	.....]	*
	(1981)	0.109	[.....	0.891	.....]	*
$H_{2(34)5}$	(1980)	0.117	[....	0.883	....] 0.000	*
	(1981)	0.104	[....	0.892	....] 0.000	*
H_{2345}	(1980)	0.120	0.213	0.667	0.000	*
	(1981)	0.110	0.361	0.181	0.348	*
With out-population						
$H_{2(345)8}$	(1980)	0.119	[.....	0.339	.....]	0.543
	(1981)	0.122	[.....	0.779	.....]	0.099
$H_{2(34)58}$	(1980)	0.119	[....	0.735	....] 0.000	0.146
	(1981)	0.122	[....	0.811	....] 0.000	0.135
H_{2345B}	(1980)	0.123	0.245	0.426	0.000	0.206
	(1981)	0.123	0.003	0.770	0.000	0.104

bank program has been met. The two analyses differ, however, in the estimated contributions of the other stocks. For example, the GSI-estimated contributions of the Spring Creek [SC] and Snake River [TU and DW] stocks are 7 and 8% for the 1980 collection, respectively (Milner et al. 1985). The corresponding estimates are 0.9 and 0% for the present treatment (H_I or H_{I8}). The differences in estimated contributions for these stocks by the two methods (14% for the two stocks) are great enough to have management implications. In a large fishery, even a small percentage contribution may represent a substantial number of fish — perhaps too many from depleted stocks with small run sizes.

There are three possible factors that might account for the difference: (a) the treatment of source population allele frequencies, (b) the pooling strategy for the Upper Columbia sources, and (c) the treatment of the IDH and MDH isoloci. For the standard GSI treatment, with allele frequencies of the source populations fixed at the observed levels, there is a small inflation of the estimated m_i-values of the minor contributing stocks (Fournier et al. 1984; Beacham et al. 1985). Our validation results (Table 2) suggest that there will be similar (small) biases in our estimates, and the difference we see (~14%) is probably too large to be accounted for in this fashion. We showed earlier that the pooling strategy for potential source populations could have an effect on the estimates, and that pooling [PR] with [WB] and [VB] — as was done for the GSI analysis — is probably not good practice. Some of the distortion in estimated m-values for [SC] and the Snake River sources [TU] and [DW] may be the consequences of inappropriate pooling. Probably the most important factor, however, is the different treatment of isoloci in the two studies.

Recall that we have treated the segregation of variation at isoloci as due to a single locus, whereas the current GSI method treats the variation as due equally to a pair of loci with equal allele frequencies. Waples (1988) has shown that the usual treatment leads to biases in allele frequency estimates; those biases would translate, in turn, into biased m-values from the mixture analysis. Our practice of attributing all of the variation to a single locus is almost surely a better strategy for the loci and genotype frequencies presented here, but is also probably not the generic solution to the problem of isoloci. Ultimately, we will need to extend the mixture analysis for genetic loci showing various sorts of dominance and other sorts of phenotypic ambiguity. Those extensions are logically straightforward but elaborate enough to justify postponement to a later effort.

Poor composition estimates are not restricted to minimally-contributing stocks; they may also result wherever two (or more) stocks are genetically very similar. This fact is cogently demonstrated both by our contrived mixture of the two Ice Harbor Dam collections [TU and DW], illustrated in Fig. 2b, and by the results of the egg bank analyses for the Upper Columbia sources [WB, VB, and PR]. The analysis is largely indifferent to the allocation of m_i-values among genetically similar stocks, although the total estimated contribution to the combination of such sources is reasonably accurate. This situation is predictable, since a χ^2 contingency test of the differences among potentially confounded stocks is small. Confounding also becomes evident in the course of the analysis; the estimated m_i-values vary considerably from model to model, an indication of unstable estimates. Relative to the egg bank collections, it seems clear that some combination of the three Upper Columbia stocks [WB, VB, PR] is providing the largest contribution, but that no great reliance should be placed on the precise allocation of m_i-values among the three stocks.

Interestingly, these three stocks represent a single management unit, so the total contribution for the trio (the estimate for which is robust to the choice of model) is the feature of interest. This will not always be true, of course, but we note that there is a general tendency for stocks from a restricted watershed (sometimes defined as a single management unit) to be genetically very similar, if not indistinguishable (Waples and Smouse 1990). In any case, some preliminary analysis of the genetic similarity of the potentially contributing stocks would be generally useful. Wherever very similar stocks can be pooled into meaningful management units, some judicious pooling is in order. The added advantage of this strategy is that we can increase the sample sizes of the stocks, while reducing the dimensionality of the estimation problem, sharpening the resolution of the analysis.

Finally, we return to the questions raised at the outset. Using our new analysis, (1) what is the effect of treating baseline frequencies as random variables instead of parameters? We weight the genetic evidence from each stock according to sample size; some source population allele frequencies are estimated with more precision than are others. There is additional information in the harvest catch about the source population allele frequencies; we use it, whereas the current GSI model does not. We can allow for the occurrence in the mixed catch of an allele not seen in a particular source; we merely assume the allele is (parametrically) present but too infrequent to have shown up in the sample from the stock. We can also deal in a particularly convenient way with holes in the data; we put in an iterated 'missing value' for the hole. Finally, and most important, we can extend the analysis to include one or more unsampled out-populations, for which we have no baseline data at all. The ability to search for something we have missed in our baseline samples is a major addition of the new analysis. (2) Under what circumstances can we reject the null hypothesis that the mixture contains only stock A (or only A and B, etc.)? We have shown that the analysis is sensitive enough to detect additional components as long as they occur in sufficient numbers and are genetically different

enough to be recognizable. Within a management unit, we do not have much resolution, but between units, we have sufficient power to detect additional contributors. In a more general vein, the larger the contribution and the more genetically different is an additional contributor, the more likely we are to be able to detect it. (3) Relative to the egg bank harvests, do we find any evidence that unsampled stocks contribute meaningfully to the harvest? We would have a difficult time detecting out-populations that were genetically similar to those sampled, say additional Deschutes River stocks similar to that already included in the analysis, but we can say that there seem to be no managment units that have been overlooked, and we can be fairly confident that the endangered Snake River stocks have not been further depleted by the Bonneville Dam egg bank collections.

In closing, we should say a few words about the scope of the analysis. We have here examined a fishery that involves a small number of potential sources, and find that a combination of two out of four management units contribute. For illustrative purposes, our choice was ideal, small enough to be manageable but complex enough to be a challenge. For chinook salmon, however, this is a small version of a much larger problem; many hundreds of stocks may contribute to some of the oceanic fisheries.

While the analysis described here can be extended to almost any size, the sheer scale of the problem quickly becomes unmanageable. Note, for example, that we are here estimating 18 allele frequency parameters (12 loci) for each of the potential source populations, both those represented by baseline samples and those invoked for the unsampled out-population. Leaving aside the limiting question of statistical identifiability for a mixture model, the sheer size of the iterative estimation effort with an increasing number of potential stocks is almost prohibitive. For the oceanic fisheries, some judicious pooling of source populations would seem to be a practical necessity, but is not without some risks. With a little care in the choice of which populations to pool, however, the biological situation lends itself naturally to this strategy. Recall that we had difficulty distinguishing among genetically similar stocks within the same management area (e.g. within the Hanford Reach unit and within the Snake River unit), but we had no difficulty distinguishing among management units.

Waples and Smouse (1990) have shown that for chinook salmon, genetic differences within management units are small, relative to those between them. It is also well known that the genetic differences between management units within major watersheds (the Columbia, the Sacramento, the Fraser, etc.) are small, relative to the average genetic differences among the watersheds (Utter et al. 1989; Waples and Smouse 1990). Our results suggest that some judicious pooling of stocks within management units will reduce the scope of the effort, without creating any undue problems for the mixture analysis. Moreover, while straying is known to occur, it is usually localized (Ricker 1972; Lister et al. 1981), having a minor impact on genetic composition. For management purposes, fine detail on this scale is often not necessary. Given large genetic differences among major watersheds, we might even be tempted to ignore management units within them for the wide-ranging oceanic harvest, but Wood et al. (1987) and Mulligan et al. (1988) have shown that this can lead to the same trouble (on a larger scale) that we encountered when pooling [PR] with [WB] and [VB].

While the potential difficulties in expanding the scope of the analysis require further study, there are numbers of situations in which the methods described here can be put to immediate use. Two examples will suffice. First, several major river systems in northwestern North America support terminal fisheries for pacific salmon. In some cases (e.g. the chum and chinook salmon fisheries in the Yukon River), potential source populations are so remote that exhaustive baseline sampling is not feasible. The unconditional likelihood model can be used to evaluate in-river catches for the presence of major populations not included in the set of available baselines. The same approach can be used in other river systems not supporting fisheries by sampling juveniles or returning adults near the mouth.

Second, there are analogous problems for salmon caught in international waters by high seas driftnet vessels. Several recent seizures of illegally-caught salmon have emphasized the magnitude of the problem, and it is of considerable interest to determine the countries (or even the continents) of origin for the catch. The National Marine Fisheries Service has efforts under way to apply GSI methods to high seas catches of chum salmon; those efforts are hampered by incomplete baseline data from source populations in Japan and the USSR. We expect the unconditional likelihood approach developed here to play an important role in evaluating the adequacy of the Asian baselines as we progressively acquire genetic data for new source population samples.

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Determination of Fish Movement Patterns from Tag Recoveries using Maximum Likelihood Estimators

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Hilborn, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Can. J. Fish. Aquat. Sci. 47: 635–643.

A general method for analysis of movement data from tag returns is proposed which has four major components: (1) a population dynamics and movement model that describes how the number of tagged individuals in each spatial location changes over time; (2) an observation model which describes how the tags are recovered and reported; (3) a likelihood function that specifies the likelihood of observing a specific number of recoveries in each space/time stratum as a function of the number thought to be there under a specific set of parameters of the population dynamics, movement and observation models, and (4) a nonlinear function minimization computer algorithm. This approach is applied to movements of skipjack tuna (*Euthynnus pelamis*). When tagging and recapture take place in each spatial stratum, reliable estimates of movement rates can be obtained. The approach described is completely general and can be used in cases where movement takes place continuously, or only once in the life history. Methods for determining confidence limits and evaluation of residuals are presented and extensions that include tagging mortality, tag shedding, and size specific vulnerability are discussed.

Une méthode générale d'analyse des données portant sur les déplacements à partir des bagues retournées est proposée : cette méthode compte quatre éléments importants : (1) un modèle de mouvement et de dynamique des populations qui décrit comment la population constituée par le nombre de sujets marqués dans chaque emplacement spatial, se transforme avec le temps; (2) un modèle d'observation qui décrit comment les bagues sont récupérées et rapportées; (3) une fonction de vraisemblance qui détermine la vraisemblance de l'observation d'un nombre donné de récupérations dans chaque strate spatiale-temporelle en fonction du nombre qu'on estime être présent en vertu d'un ensemble précis de paramètres retenus pour les modèles de la dynamiques des populations, des mouvements et des observations; enfin, (4) un algorithme de minimisation de la fonction non linéaire. Cette approche est appliquée aux déplacements de la thonine (*Euthynnus pelamis*) à ventre rayé. Avec le marquage et le recapture dans chaque strate spatiale, il est possible d'obtenir des évaluations fiables des taux de déplacement. L'approche décrite est on ne peut plus générale et peut s'appliquer aux cas de déplacements continuels ou aux cas d'un seul déplacement dans la vie. Les méthodes utilisées pour déterminer les limites de confiance et l'évaluation des résidus sont présentées; il est question aussi de la mortalité par marquage, de la perte des bagues et de la vulnérabilité associée à chaque taille.

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Many animals are highly mobile. Individual birds, mammals, and fish have been known to move over 10 000 km and there are entire populations, such as grey whales and many arctic breeding birds, whose annual migration cover similar distances. In some cases one can track such populations, or more rarely an individual, over long distances. More commonly, however, our knowledge of long distance movements of animals comes from tagging studies.

This is particularly true of fish, where it is beyond current technology to track individuals very far. Tagging data tell us where tagged fish were released and where they were recovered. Since most large scale tagging studies rely on commercial capture of tagged fish, multiple recaptures of individuals are rare; the fish are either dead or too valuable to return to the water.

Fisheries managers and biologists want to know the movement patterns of populations or individuals to assess the interaction between fisheries in different spatial locations and to define the discreteness of stocks. Tagging studies, though, are often the only way to assess total stock size, natural and fishing mortality, so that determination of movement often becomes a secondary goal only. Nevertheless, there is now a large body of tagging data for fisheries around the world which provides the basis of most of our current knowledge of fish movement.

Once a fisheries biologist has collected tagging data from a population, he must decide how to use this information to reveal fish movements. The most commonly used technique is to draw arrows from where fish were tagged to where they were recovered.

Occasionally more quantitative analyses are used. For instance, one can plot the distance travelled versus time since release (Schaefer et al. 1961). One obvious problem in the analysis of tag recoveries is that in areas without fishing effort no tags are recovered, or more generally, the number of recoveries is related to the fishing effort in that area. To compensate for this, recoveries per unit of fishing effort are used rather than total recoveries. The Inter-American Tropical Tuna Commission has analyzed tagging data in this way (Bayliff 1979), using measures of directional and random movement developed by Jones (1959, 1976).

A major problem with most of these methods of analysis is that no account is taken of the probability of capture between the time of release and the location of recovery. Few fish may be caught in a certain area simply because there is a high probability of capture along the way. Secondly, the methods (with the exception of Jones' method) do not state a specific hypothesis about fish movement and then attempt to estimate the parameters and validity of that hypothesis. Jones' method suffers because it allows only for random or simple directional movement.

There has been remarkably little formal statistical work on analysis of movement data. Darroch (1961) and Arnason (1972, 1973) examined spatially stratified capture recapture models, but only for the case with multiple recaptures. As noted in Schwarz and Arnason (1990), these studies assumed equal probability of capture in all areas. Further, these approaches are not applicable to most fisheries tagging studies in which individuals are recaptured once by a commercial fishery and recovered dead. Only recently has attention turned to using the traditional models and approaches of mark–recapture studies as summarized in Burnham et al. (1987) on spatially structured problems with unequal fishing effort in the spatial strata.

Ishii (1979) used a model of movement in which he specifies a Markovian movement model between geographic areas in the eastern tropical Pacific. He simulated the movement of tagged fish and used nonlinear minimization techniques to find the movement probabilities that minimize the difference between observed and expected number of recoveries in each spatial area. Ishii's model includes natural mortality and tag shedding as parameters to be estimated simultaneously with movement.

Sibert (1984) modeled natural mortality, fishing mortality, and movement between two countries, Papua New Guinea and the Solomon Islands. He used tagging data to determine the mortality rates and exchange rates between the two counties. Like Ishii, he estimated the parameters with least squares.

These two papers constitute a new approach to the analysis of animal movement data, but are unknown beyond a small circle of tuna biologists. For example, in a major review of tuna movement patterns (Hunter et al. 1986), there is no reference to Ishii's work. This is probably because Ishii's and Silbert's papers were published in rather obscure locations as specific case examples rather than general approaches. Recently, Schwarz (1988) and Schwarz and Arnason (1990) described extensions of the traditional statistical analysis of mark–recapture using explicit multinominal probability functions.

In this paper I present a general framework for the analysis of animal movement, natural mortality, and harvest from tagging data and show that Ishii's and Sibert's studies are special cases of the same approach. Their heuristic least squares approach is replaced here by a more rigorous maximum likelihood method based on the Poisson distribution. Two examples are presented and a number of potential extensions and modifications of the method are discussed. The method I present has a number of significant features: (1) it is applicable to nearly any tagging study, (2) it requires no detailed statistical derivations, but relies instead on nonlinear search techniques to minimize a simple likelihood, (3) it is easily implemented on microcomputers with a few hours programming time.

General Framework

I define the following symbols to be used in this section.

T_{iat} = the number of tags released from tag group i, area a, time t
$\mathbf{T}$ = a matrix of all the T_{iat} values
$\hat{N}_{iat}$ = the predicted number of tagged fish of group i present in area a at time t
R_{iat} = the number of tags recovered from tag group i, area a, time t
$\mathbf{R}$ = a matrix of R_{iat} values
$\hat{R}_{iat}$ = the predicted number of tags recovered from tag group i, area a, time t
$\hat{\mathbf{R}}$ = a matrix of R_{iat} values
$\mathbf{x}$ = a vector of parameters of the population dynamics and movement model
$\mathbf{y}$ = a vector of parameters of the observation model
p_{ij} = probability of movement from area i to j
E_{at} = fishing effort in area a, time t
q_a = catchability coefficient in area a
h_{at} = harvest rate in area a, time t, $(= E_{at} q_a)$

A tag group i for my analysis is defined as a group of fish tagged in the same space and time stratum, but could be extended to include size groups, sex, or whatever criteria are thought to be important in movement, survival, and probability of capture. In this analysis I write all equations in discrete space and time. The same models can easily be transformed to continuous equations and solved in exactly the same fashion.

My approach for the analysis of tagging data has four elements: (1) a population dynamics and movement model, (2) an observation model, (3) likelihood of recoveries, and (4) a nonlinear function minimization procedure.

Population Dynamics and Movement Model

A simulation model for the survival and movement of tagged individuals must be specified. This must include natural and fishing mortality as well as movement and could include tagging mortality and tag shedding. If fish vulnerability is size related, growth may need to be a specific part of this model.

If we consider the dynamics in n areas, each connected by a Markovian exchange process, the following model could be used.

$$(1)\quad \hat{N}_{iat+1} = \sum_{j=1}^{n} (\hat{N}_{ijt}(1-h_{jt})p_{ja}) + T_{iat}$$

$$h_{at} = E_{at}\, q_a$$

Given the known tag releases $\mathbf{T}$, the fishing efforts E_{at}, and the p and q values, we can predict how many individuals would be alive from each tag group in each area. While equation (1) does not explicitly allow for a survival from natural mortality term, natural mortality is implicit when the $\Sigma_j p_{ij}$'s for an area do not sum to 1.0. No allowance for higher mortality among fish that are moving is provided, but this also could be added.

Observation Model

A model is required that specifies the relationship between the tagged fish predicted to be in an area under equation (1) and the tagged fish that are actually captured and reported to the management agency. In its simplest form this is the predicted number of tagged fish harvested, as taken from the population dynamics model, but can include nonreporting of tags, misreporting, and tag loss.

If we assume that harvest rate is proportional to fishing effort, and that all tags that are captured are returned, then equation

(2) below is the specific observation model for our n area Markovian movement model.

$$(2)\quad \hat{R}_{iat} = \hat{N}_{iat}\, q_a E_{at}$$

Likelihood of Recoveries

Given the tag release data, and the population dynamics and movement model of equation (1), we know how many tagged fish we expect to be in each area at each time from each tagging group. Using equation (2) we know how many recoveries to expect from each group, in each area, at each time. We thus have a matrix of predicted recoveries $\hat{\mathbf{R}}$ for each tag release group by time and area. We also have a matrix of observed recoveries $\mathbf{R}$. We want to calculate the likelihood of the observed recoveries $\mathbf{R}$ given the parameters of our population and observation models, that is

$$(3)\quad L(\mathbf{R}|\mathbf{p}, \mathbf{q}, \mathbf{E}, \mathbf{T})$$

which using equations (1) and (2) becomes

$$(4)\quad L(\mathbf{R}|\hat{\mathbf{R}})$$

which is the product of all the individual likelihoods for each tag group, space, and time stratum.

$$(5)\quad \prod_i \prod_a \prod_t L(R_{iat}|\hat{R}_{iat})$$

A statistical likelihood or probability model must be developed that calculates the likelihood of the number of recoveries actually being reported if the population dynamics and observation models are true.

There are two traditions in maximum likelihood estimation in the analysis of tagging data. The use of explicit multinomial calculations dominates; almost all of the methods described in Burnham et al. (1987) rely on specifying an explicit model of tag survival and recovery, then writing the probability of recoveries as an explicit multinomial of the parameters of the model. The recoveries in each stratum are expected to be multinomially distributed. The second tradition is found primarily in the use of generalized linear models (Chapman 1948; Cormack 1981; McCullagh and Nelder 1983) in which the number of expected recoveries in each stratum is expected to be Poisson distributed. My method follows this school. Because there is a low probability of any individual tag being recovered in any space/time stratum, the multinomial can be approximated by the Poisson.

The Poisson distribution for an individual tag group, space, and time can be written as

$$(6)\quad L(R_{iat}|\hat{R}_{iat}) = \frac{e^{-\hat{R}_{iat}}\, \hat{R}_{iat}^{R_{iat}}}{R_{iat}!}\ .$$

The total likelihood for all observed recoveries given the parameters of the population dynamics and observation models, and the number of tags released ($\mathbf{T}$) is thus

$$(7)\quad L(\mathbf{R}|\mathbf{p}, \mathbf{q}, \mathbf{E}, \mathbf{T}) = \prod_i \prod_a \prod_t \frac{e^{-\hat{R}_{iat}}\, \hat{R}_{iat}^{R_{iat}}}{R_{iat}!}$$

Nonlinear Function Minimization Procedure

A nonlinear function minimization procedure is necessary to find the values of the population dynamics and observation models that maximize the likelihood of the observations given the parameters of the model. This type of computer program is commonly available on minicomputers and growing in availability on microcomputers. The standard reference is Bard (1974) and an easily implemented BASIC computer program is described in Schnute (1982).

Comparison to Other Methods

The above approach is quite similar to the Ishii (1979) model, except it is much more general and uses maximum likelihood, rather than least squares. My approach is fundamentally an extension of the generalized linear model approach of Cormack (1981), but is extended in two ways. First, by adding a spatial dimension to the model we are able to estimate movement patterns. Second, the generalized linear model approach is quite confining in the models it can consider, and my approach breaks this confinement to allow models that cannot be written in a linear form by using a general nonlinear search algorithm instead of the computer code for linear models. However, the basic framework of predicting recoveries in each space/time stratum is identical to that used by Cormack.

My approach is closely related to the multinomial maximum likelihood estimators for analysis of tag returns. The multinomial equivalent of equation (7) is (Seber 1982 page 131):

$$(8)\quad L(\mathbf{R}|\mathbf{p}, \mathbf{q}, \mathbf{E}, \mathbf{T}) = \prod_i \left(\left[\frac{(\Sigma_{at} T_{iat})!}{(\Pi_a \Pi_t R_{iat}!) m_i!} \right] \times \left[\prod_a \prod_t v_{iat}^{R_{iat}} \right] w_i^{m_i} \right)$$

where

$$v_{iat} = \frac{\hat{R}_{iat}}{\Sigma_{at} T_{iat}}$$

$$w_i = \frac{m_i}{\Sigma_{at} T_{iat}}$$

where m_i is the number of tags from release group i that were never recovered. The numerator of the left hand term is the total number of tags put out in group i, the first term in the denominator is the product of all the actual recoveries for tag group i, and the second term in the denominator is all the tags never recovered. The term v_{iat} is the proportion of tags of group i that are expected to be recovered in area a time t, and the term w_i is the proportion of all tags from group i expected to be not recovered. The multinomial likelihood is as easily implemented as the Poisson for the types of movement models described here.

Thus, one can use my methodology, but instead of following the school of Chapman, McCullagh and Nelder, and Cormack, follow the multinomial approach which fills the pages of Seber (1982) and Burnham et al. (1987). We substitute the use of the multinomial likelihood for the Poisson.

I have performed a number of Monte-Carlo experiments comparing the Poisson and multinomial approaches, and they produce effectively identical answers. The multinomial and Poisson will only differ when the probability of capture in a single space–time strata is not small. Computational convenience rather than philosophical viewpoint should govern the choice of approach.

This simulation approach represents a break with tradition. The normal approach is to algebraically derive the v and w values. My approach calculates them by simulation. The simulation approach is primarily advantageous when the models become complex, as most movement models are. Indeed, the movement models with more than two spatial areas would

TABLE 1. Estimates of catchabilities (q's), and movement rates from the present analysis, Sibert (1984), and Kleiber et al. (1983). The other column includes both natural mortality and movement to other areas. The Kleiber et al. analysis was done on a fishery-by-fishery basis and does not estimate movement, so we call their total loss rate term 'other'. The movement parameter from PNG to PNG is $2p_{11} = 0.71$, movement from PNG to SOL is $p_{12} = 0.0001$, movement from SOL to PNG is $p_{21} = 0.0031$, and the movement from SOL to SOL is $p_{22} = 0.9$.

		Movement probabilities To		
	From	PNG	SOL	Other
Present analysis				
$q_{PNG} = 0.000084$	PNG	0.7100	0.0001	0.2899
$q_{SOL} = 0.000022$	SOL	0.0031	0.9000	0.0969
Sibert (1984)				
q_{PNG} 0.000160	PNG	0.5900	0.0340	0.376
$q_{SOL} = 0.000032$	SOL	0.0130	0.9280	0.059
Kleiber et al. (1983)				
$q_{PNG} = 0.000090$	PNG	0.5300		0.470
$q_{SOL} = 0.000056$	SOL		0.8400	0.160

require enormous algebraic expenditure. The complexity of the algebra increases geometrically with both the number of areas and the number of times, so that a seven area model with movement between each area for 20 time periods would not only be tedious, it would be impossible. This is much more satisfactorily replaced with a few lines of computer program.

A Two-Fishery Tag Exchange Model for Skipjack Tuna

As a first example I analyze the Papua New Guinea (PNG)-Solomon Islands (SOL) data presented in Sibert (1984). These two counties are major tuna fishing nations in the western Pacific. Fish tagged in each fishery were known to move to the other fishery, but also to different fisheries not included in the analysis. For simplicity, and unlike Sibert, we will ignore tagging mortality, tag shedding, and nonreporting of tags. The population dynamics model is thus:

$$(9)\quad \begin{aligned} \hat{N}_{i1t+1} &= \hat{N}_{i1t}(1-h_{1t})p_{11} + \hat{N}_{i2t}(1-h_{2t})p_{21} + T_{i1t} \\ \hat{N}_{i2t+1} &= \hat{N}_{i2t}(1-h_{2t})p_{22} + \hat{N}_{i1t}(1-h_{1t})p_{12} + T_{i2t} \\ h_{1t} &= E_{1t}\,q_1 \\ h_{2t} &= E_{2t}\,q_2 \end{aligned}$$

where $\hat{N}_{iat+1}$ is the number of fish from tag group i predicted to be alive in area a at time $t + 1$, h_{1t} is the fishing mortality rate in area 1 at time t, T_{iat} is the number of tags released for tag group i in area a at time t, and the $p'_{ij}s$ are the proportion moving from one area to another. In this analysis there are two tag groups; one group released in Papua New Guinea, and one group released in the Solomon Islands. E_{at} is the fishing effort in area a at time t, and q_a is the catchability coefficient in area a.

Note that implicit in this model is the potential for the p's for each area to not add to 1 because of movement to other areas and natural mortality, which are indistinguishable. If, for instance, $p_{11} + p_{12} = 0.72$ (as they do in Table 1) then 28% of the individuals either die to natural mortality or move to areas other than the Solomon Islands. There are thus six parameters to be estimated in the population dynamics model, four p's and two q's. These may be confounded.

TABLE 2. Estimated fishing mortalities, catchabilities, and movement probabilities for seven-fishery model. Fishery codes are PAL = Palau, YAP = Yap, INT = Interntional waters between the Federated States of Micronesia (YAP, TRK, PON), Palau, PNG, and Indonesia, TRK = Truk, PON = Ponape, PNG = Papua New Guinea, SOL = Solomon Islands, OTH = loss of tags to other areas and natural mortality. For all countries except PNG and SOL the fishing mortality (F) is estimated (effort assumed constant at 1.0; for PNG and SOL the catchability coefficient q is estimated since effort data were available). If a 0 appears in the movement probability table, it means that these countries are not adjacent and no direct exchange rate was estimated unless an * appears, in which case it means the best estimate was that no exchange occurs between countries. The lower portion of the table constitutes the p matrix, with the exception of the "other" column which is calculated as one minus the sum of the other columns for each row and represents both natural mortality and movement to other areas.

	PAL	YAP	INT	TRK	PON	PNG	SOL
F or q	.0049	.0043	.0046	.0054	.0065	.00012	.00003

	Probability of movement To							
From	PAL	YAP	INT	TRK	PON	PNG	SOL	OTH
PAL	0.677	0.047	0.107	0	0	0	0	0.168
YAP	0.008	0.707	0.032	0.041	0	0	0	0.211
INT	0.008	0.041	0.808	0.100	0.00*	0.034	0	0.008
TRK	0	0.066	0.027	0.635	0.084	0	0	0.187
PON	0	0	0	0.082	0.683	0.00*	0	0.235
PNG	0	0	0.052	0	0.00*	0.600	0.013	0.336
SOL	0	0	0	0	0	0.024	0.873	0.124

The observation model is:

$$(10)\quad \hat{R}_{iat} = \hat{N}_{iat}\,q_a\,E_{at}$$

which has no additional parameters beyond those in the population dynamics model. I assume that 100% of the tags were returned, and use the Poisson likelihood function as the likelihood.

This analysis (Table 1) differs from the analyses of Sibert (1984) primarily in that my estimated loss rate in PNG is considerably lower. This is probably due to the use of the maximum likelihood estimator which assigns more weight to the few recoveries that took place more than a year after marking.

Extension to Seven Fisheries

We can expand the previous analysis to include a much larger geographic area. The skipjack survey and assessment programme of the South Pacific Commission tagged over 150 000 skipjack tuna throughout the western Pacific from 1977 to 1981 (Kearney 1983). Figure 1 shows the part of the western Pacific under consideration. Skipjack were tagged in all jurisdictions except Indonesia in Fig. 1 and most tags were recovered in this area. Tagging and recoveries from Fiji are the major data excluded from the current analysis.

The model for this analysis is the general n area Markovian model given in equation (1), and is the same as the two area model of the previous section except instead of two-fishery exchange we consider seven fisheries. Because not all fisheries are contiguous with one another, we only estimate the exchange

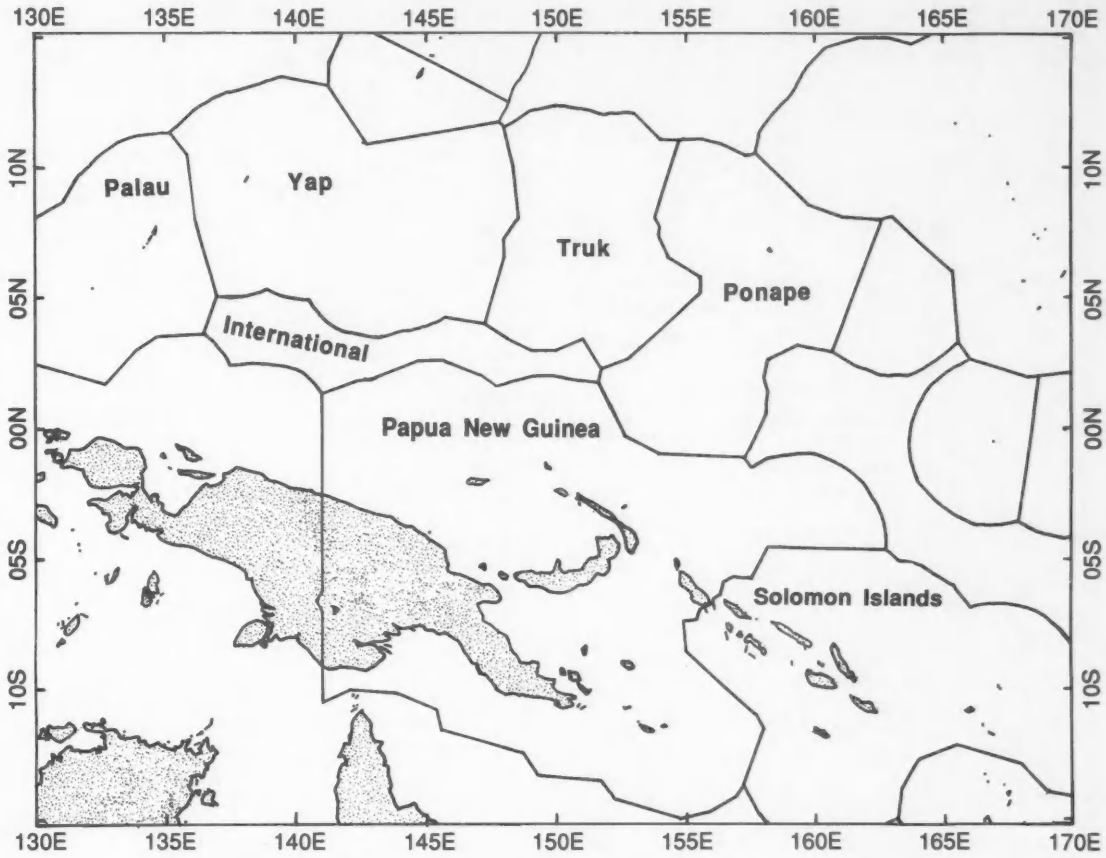

FIG. 1. Map showing major tuna fishing countries of western Pacific used in seven-fishery tag analysis model.

rate between contiguous fisheries, which reduces the number of movement parameters to be estimated from $7 \times 7 = 49$ to 25. We thus assume that it takes a minimum of 2 mo for a fish to move from one area to a noncontiguous area. No fish are known to have moved between noncontiguous areas in a 1-mo period and with the movement rates between contiguous areas generally low (< 0.10 per month), noncontiguous movement in 1 mo is unlikely enough to be safely ignored. Fishing effort data were available for PNG and SOL only, so I assumed effort was constant at 1.0 in all other areas. The q estimated for the other counties becomes, in fact, the monthly fishing mortality rate. Even in PGN and SOL, the effort data were not complete over the time period of tagging and recovery (October 1977–December 1981).

Data

I defined each tag group as fish released during a single month in a specific fishery. During the skipjack program there were 18 tag groups in the area considered in this analysis. Fish were tagged in all areas except international waters. All release, recovery, and effort data are available from the author.

We consider only recoveries from the seven countries included in this model. There were recoveries outside the region, particularly a few tags from Palau and PNG recovered in Indonesia, but these were ignored and in effect become another form of unaccounted for disappearance that includes natural mortality and movement to other areas.

Results

The fishing mortality rates (Table 2), are about 0.005 per month, a figure consistent with previous estimates for countries other than PNG and SOL. The catchabilities for PNG and SOL are close to the previous estimates from Table 1. The movement probabilities show no great surprises, but are very interesting nevertheless. The results for PNG and SOL are essentially the same as we found in the two area model; indeed these countries seem remarkably isolated from the rest of the western Pacific. PNG has an extremely high loss rate, but the tags do not seem to go to the other countries considered in this model. Seven fish tagged in PGN were recovered in Indonesia, but these recoveries were not included in the analysis since we have no knowledge of the time pattern of fishing effort or probability of tag returns from Indonesia.

Loss to natural mortality and other areas is rather low; with the exception of PNG it is usually below 25% per month. Kleiber et al. (1983) estimated the natural mortality rate over the

entire skipjack data set at 17% per month. If one believes in a uniform natural mortality rate for skipjack, then the very low total loss rates from SOL, international waters, Truk, and Palau would suggest that the natural mortality rate must be much lower, perhaps around 10% per month.

Potential Modifications

Generalization of Population Dynamics and Observation Models

The models presented so far have been discrete Markovian movement models. The basic approach can be generalized to a very wide variety of models, which can be written as:

$$(11)\quad \hat{N}_{iat} = f(\hat{N}_{i1\ldots nt-1}|\mathbf{x}, \mathbf{T})$$

where f is the population dynamics model, the parameters of which could include natural mortality rate, vulnerability to fishing gear, and movement probabilities, as well as tagging mortality, tag shedding, and growth. In the simplest case, for a single release group in each area, the subscript i denotes area of tagging, but could include time of tagging, size at tagging, etc.

The observation model can be generally written as:

$$(12)\quad \hat{R}_{iat} = g(\hat{N}_{iat}|\mathbf{y})$$

where $\mathbf{y}$ are the parameters of the observation model that could include tag return rates and tag reading error.

The seven-fishery model presented earlier could easily be modified to represent a general geographic square model, where any size geographic units were used. For tuna, a 5° square basis might be appropriate. Many tuna agencies, particularly the Inter-American Tropical Tuna Commission (IATTC) have databases on tagging, recaptures, and efforts that may well be amenable to this type of analysis.

A number of alternative models would be possible with this type of geographic data. The simplest would be a diffusion model with one movement parameter and one survival rate to estimate. In discrete form (and ignoring harvesting) this could be written:

$$(13)\quad N_{i,j,t+1} = N_{i,j,t}s - 4sdN_{i,j,t} + sd[N_{i+1,j,t} + N_{i-1,j,t} + N_{i,j+1,t} + N_{i,j-1,t}]$$

where d is the proportion of individuals that move from one square to an adjacent square each time period and s is survival from natural mortality. This representation is a finite difference approximation to the normal two dimensional diffusion equations described extensively in Okubo (1980) and used to model tuna movement in Hilborn (1987):

$$(14)\quad \frac{\partial N}{\partial t} = -(1-s)N + D\left[\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}\right]$$

The parameter D is the analog of d from the finite difference equations.

For discrete square models, a slightly more refined movement model would be one in which there were four movement parameters to be estimated: the proportions moving to the square to the north, the square south, the square west, and the square east. This would include the possibilities of diffusion connected with a general drift model. Note that both of these geographic movement models would require very few parameters to be estimated relative to the more complex movement model used for the seven-fishery model.

A further extension of the geographic square model (or any movement model) would be to allow for temporal or spatial stratification. Thus, in the seven-fishery model we could have stratified the year into two periods and used different movement probabilities for each time of year. This would produce a rather large number of parameters in the seven-fishery model, but for the simpler geographic square models discussed in the preceding section, one could include seasonal variation in movements without too many parameters. This type of analysis might be most useful for truly migratory species that engage in an annual north–south movement. North Pacific albacore tuna (*Thunnus alalunga*) are a possible example.

Spatial stratification would also be possible. For instance, in the eastern Pacific, fish marked close to land appear to move less than those marked far at sea. One might use the general directional diffusion model discussed in the preceding section, but spatially stratify the geographic area into three to six areas with different movement parameters. While the calculations might remain on a 1 or 5° basis, the movement parameters would be stratified on a larger and biologically more meaningful scale.

Size-Specific Probabilities of Capture

In some fisheries, particularly gillnet fisheries, the probability of capture is size-specific. Nick Dow (Victoria Department of Fisheries, Queenscliff, Victoria, Australia) has been using similar models to those described in this paper, where he estimates simultaneously the size selectivity, growth, movement, natural and fishing mortality. This requires treating each individual fish as a tag group, since each fish has a unique size and will therefore have unique capture and growth probabilities.

Tag Mortality, Shedding, and Nonreporting and Confounding of Parameters

Three common problems with tag analysis are the potential for tagging mortality, tag shedding, and nonreporting of tags. In the models described above we have ignored these problems. However, they can be incorporated in a very straightforward manner.

Tag mortality could be considered by adding one additional parameter: the number of tags released and followed through the simulation would be the number actually released times 1.0 minus the tagging mortality rate.

Tag shedding could be considered by adding an additional parameter, yet it is normally indistinguishable from natural mortality. The method to determine tag shedding is to use double tag experiments, which could also be easily added to our analytic framework. There will then be the likelihood of recovering one and two tags from doubly tagged individuals. Nonreporting of tags could also be an additional parameter to be estimated, but this is algebraically indistinguishable from tagging mortality. Both are normally (Kleiber et al. 1983) estimated as a single parameter.

While it is conceptually and practically straightforward to add tag mortality, shedding, and nonreporting, these parameters will normally be highly or totally confounded with fishing mortality, natural mortality, and movement. Similarly it is theoretically possible to estimate temporal variation in natural mortality or catchabilities, but in practice these may prove difficult if not to impossible to identify.

TABLE 3. Parameter correlations for two-fishery model estimated by inverse Hessian method.

	PNG-q q_1	SOL-q q_2	PNG-PNG-p_{11}	PNG-SOL p_{12}	SOL-PNG p_{21}
SOL-q q_2	−0.09				
PNG-PNG p_{11}	−0.83	0.11			
PNG-SOL p_{12}	0.22	−0.07	−0.26		
SOL-PNG p_{21}	−0.09	0.20	0.01	−0.08	
SOL-SOL p_{22}	−0.09	−0.83	−0.10	−0.12	−0.25

Confidence Intervals

We would clearly like some idea of our confidence in the parameters estimated from these analyses. I can suggest two possible approaches. The first is the use of the inverse-Hessian matrix as a linear approximation to the confidence intervals (Bard 1974). This method looks at the derivative of the likelihood function with respect to the parameters. If the likelihood is insensitive to changes in the parameter, the confidence interval for that parameter is large. Table 3 shows the parameter correlations for the parameters estimated in our two-fishery model. There is reasonably little parameter confounding (high correlations), except between the q values and the proportion staying in each fishery (−0.83 in each case). The variance–covariance matrix that emerges from this approach does not directly provide confidence intervals, although it does provide a good feeling for our understanding of parameter values and a computational framework for estimating true intervals.

The second possible approach would be some form of bootstrap analysis (Efron 1982). These methods appear to be highly reliable but are computationally intense and would require a few hundred runs of the estimation procedure. This may not be practical for most of the movement analysis we would want to consider because each run involves considerable computation time (several hours on a minicomputer). However, for the two-fishery model, such methods would be practical and would provide an easily understood confidence bound that would not depend upon quadratic approximation as does the inverse-Hessian method.

Analysis of Residuals

We can examine the deviations from our model by using the "deviance" of McCullagh and Nelder (1983). The deviance in any release group, space, time stratum is defined as:

$$(15)\quad \text{deviance}_{iat} = -2[l(R_{iat}|\hat{R}_{iat}) - l(R_{iat}|R_{iat})]$$

where $l(x|y)$ denotes the log likelihood of x given y, and in this case is the simple Poisson likelihoods as given in equation (6). The deviance is analogous to the residuals of traditional least squares and looks like an observed minus an expected likelihood squared. A large value indicates a poor fit of the model to an individual data point.

Table 4 shows the observed, and predicted number of tags recovered. The biggest individual deviance occurred at month 7 for tagged individuals released in PNG and recovered in PNG, where only six tags were recovered yet 23.66 were expected. There appear to be no major systematic deviations between observed and expected, although months 14 to 21 for tags released and recovered in SOL show considerable variability.

Discussion

The method described in this paper is easily implemented for new data sets. Biologists working with mark–release data need not be intimidated by the apparent complexity of the statistics involved in analyzing tag movements. Almost universal access to microcomputers means that any scientist involved in the analysis of a tagging program should be in a position to use these computationally intense methods to analyze tag movements.

There are a number of obvious steps in testing and developing this approach. Monte-Carlo trials need to be used extensively to determine the performance of the methods against known answers. Secondly, the approach here needs to be compared to other possibilities, particularly explicitly derived multinomial models. The approaches used in determining confidence limits also need to be developed and tested. Particularly, bootstrapping should be tried and evaluated by testing against simulated data.

At a more general level, there is the question of experimental design required to determine exchange of fish between spatial strata. I found the estimates of movement rates to be remarkably unconfounded. The experimental design involved in analysis of movement data is normally extremely powerful. The best experimental design would involve mark and release in each area, and fishing effort data by time for each area. In the seven-country model I met all of these conditions except the last. I was unable to distinguish between natural mortality and movement outside of the seven countries considered.

In contrast, Schwarz and Arnason (1990) examined a special case, in which the tagging areas were not the same as the recapture areas, and found enormous confounding of parameters. They conclude that independent estimates of population size are required. I believe their conclusions are quite particular to their special cases and have little generality. When fish are marked and released in all strata, and we do not attempt to estimate time specific or area specific natural mortality rates, the movement and fishing mortality rate parameters are quite estimable. Time specific fishing mortality rates are estimable only if we make an assumption relating fishing effort to mortality.

It would be quite useful to have a systematic exploration of what experimental designs are necessary to estimate specific parameters. This could either be done analytically or numerically. Until such work is done, I would recommend marking and recapture in each area, and estimation of fishing effort or mortality in each area.

The analysis of skipjack movement presented here must be considered very preliminary. I have used the data as examples of what can be done, rather than as a definitive analysis of this data set. I have not considered tagging mortality, or nonreporting of tags, and any thorough analysis of this data base

TABLE 4. Observed and expected tag recoveries between PNG and SOL and the associated deviance. Top half of table are data for fish tagged in PNG, the bottom half are data for fished tagged in the Solomon Islands.

	Tagged in PNG					
	Recovered in PNG			Recovered in SOL		
Month	Observed	Expected	Deviance	Observed	Expected	Deviance
1				0	.5764	1.1528
2				0	1.0102	2.0203
3	208	179.7927	4.2109	0	1.2816	2.5633
4	100	103.4803	.1185	1	1.3675	.1090
5	58	67.2392	1.3321	0	1.4437	2.8873
6	27	30.3490	.3839	2	1.4265	.2047
7	6	23.6661	18.8648	0	1.2808	2.5616
8	3	4.7817	.7663	0	1.2424	2.4849
9	0	.0000	.0000	2	1.0691	.6434
10	0	.0000	.0000	0	.0643	.1287
11	1	3.5775	2.6056	0	.0000	.0000
12	5	4.5019	.0532	0	.1257	.2513
13	1	3.7010	2.7848	1	.5026	.3811
14	2	2.4902	.1035	0	.6236	1.2472
15	3	1.7459	.7399	2	.5902	2.0620
16	7	1.1832	13.2540	1	.5258	.3373
17	5	.7002	11.0587	1	.4884	.4101
18	0	.4032	.8065	0	.4312	.8624
19	0	.2690	.5381	1	.3860	.6759
20	0	.1235	.2469	3	.3625	7.4056
21	0	.0157	.0315	1	.2526	1.2571
22	0	.0000	.0000	0	.0000	.0000
23	0	.0435	.0870	0	.0000	.0000
24	0	.0623	.1246	0	.1035	.2069
25	0	.0484	.0968	0	.2021	.4043
26	0	.0354	.0707	0	.1982	.3964
27	1	.0301	5.0651	0	.1810	.3621
28	1	.0208	5.7860	0	.1647	.3294
29	0	.0139	.0277	0	.1468	.2935
30	0	.0089	.0178	0	.1291	.2583
31	0	.0022	.0045	0	.1157	.2313
32	0	.0004	.0009	0	.9678	.1356

	Tagged in SOL					
	Recovered in SOL			Recovered in PNG		
	Observed	Expected	Deviance	Observed	Expected	Deviance
14	9	21.0244	8.7765	0	.5292	1.0584
15	28	19.8002	3.0051	0	.8709	1.7418
16	25	17.5742	2.7706	2	1.0465	.6838
17	9	16.2799	3.8911	0	.9814	1.9628
18	8	14.3465	3.3480	1	.8391	.0291
19	20	12.8238	3.4248	0	.7941	1.5883
20	16	12.0299	1.1860	0	.4999	.9997
21	18	8.3766	8.2907	1	.0085	3.1058
22	0	.0000	.0000	0	.0000	.0000
23	0	.0000	.0000	2	.3729	3.4639
24	5	3.4255	.6329	0	.6540	1.3080
25	5	6.6915	.4690	0	.6139	1.2278
26	11	6.5591	2.4931	1	.5328	.3248
27	4	5.9904	.7499	1	.5281	.3332
28	6	5.4496	.0538	0	.4161	.8321
29	2	4.8558	2.1635	0	.3093	.6186
30	0	4.2725	8.5451	0	.2166	.4332
31	0	3.8259	7.6518	0	.0058	.1164
32	1	2.2424	.8697	0	.0012	.0246

would need to do so. The lack of fishing effort for countries other than PNG and SOL may preclude a definitive analysis. Now that we know that it is possible to estimate movements from tagging data in a rigorous and reliable way, we must make sure that future tagging studies make every effort to collect the required data, which must include effort data in the recovery locations.

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REVIEWS/SYNTHÈSES

An Evaluation of the Effects of Atmospheric Acidic Deposition on Fish and the Fishery Resource of Canada

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In Canada, 7.6% of our nation's surface area is water, and approximately 38% of this is found in regions susceptible to acidic atmospheric deposition. We estimate that 390 000 lakes in eastern Canada are sensitive to acidification, and provide significant revenue through the sport fishery to the economy. Evidence indicates that Sudbury lakes and Nova Scotian rivers acidified in the 1950's, '60's, and probably early '70's. Well documented cases of loss of fish species or production due to acidification are restricted to these two regions. However, the documentation of low pH lakes in areas of high acid loading suggest that acidification is more widespread. Recent increases in pH in some Sudbury and Algoma lakes, concomitant with reestablishment of fish populations, indicates that chemical and biological recovery is possible. Evidence from diverse experimental approaches – surveys, bioassays, and whole lake manipulation – are supportive in identifying fish responses to acidification. Fish community response is dependent upon several factors: complexity of the community, stage of acidification, species sensitivity, and availability of tolerant species to invade. If replacement of extirpated species by tolerant ones occurs, total fish biomass may remain stable until critical depauperation. It is unlikely we will be able to directly document further losses due to acidification.

Le territoire canadien est constitué d'eau à raison de 7,6 % et environ 38 % de ces eaux se trouvent dans des régions vulnérables aux dépôts atmosphériques acides. On estime que 390 000 lacs de l'est du Canada sont vulnérables à l'acidification. Ces lacs, du fait de la pêche sportive, sont économiquement importants. Les données indiquent que les lacs de la région de Sudbury et les rivières de la Nouvelle-Écosse se sont acidifiés dans les années cinquante, soixante et probablement au début des années soixante-dix. Les cas bien documentés de perte d'espèces de poisson ou de perte de production causées par l'acidification sont restreints à ces deux régions. Toutefois, la documentation sur les lacs à faible pH dans les régions soumises à de fortes charges acides laissent croire que l'acidification est plus répandue. Les récentes augmentations de pH dans certains lacs de Sudbury et d'Algoma, concomittantes au rétablissement des populations de poisson, indiquent que la récupération chimique et biologique est possible. Des données provenant de diverses méthodes et enquêtes expérimentales, bio-essais et manipulations de lacs entiers facilitent la détermination de la réponse des poissons à l'acidification. La réaction des communautés de poissons dépend de plusieurs facteurs : complexité de la communauté, stade d'acidification, vulnérabilité de l'espèce et possibilité d'invasion par les espèces tolérantes. Si le remplacement des espèces disparues par des espèces tolérantes a lieu, la biomasse totale de poissons peut demeurer stable jusqu'à ce qu'il y ait un appauvrissement critique. Il est peu probable que nous puissions documenter directement d'autres pertes causées par l'acidification.

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Our scientific basis for managing pollutants in aquatic ecosystems has been derived from the application of several approaches. These include bioassays, (laboratory and in situ), "environmental impact" studies (including surveys), and the construction of models. The effects from acidic atmospheric deposition have been chronicled by Harvey et al. (1981); Haines (1981); U.S. Canada Memorandum of Intent on Transboundary Pollution (1983); Federal/Provincial Research and Monitoring Co-ordinating Committee (1986); and others. Wilk (1985) outlined the North American dilemma in

the international issue of atmospheric deposition and stressed the need for scientists to act as impartial sources of information. We agree with Schindler (1987) who suggested that ecologists should assume greater responsibility in both developing a brand of science more effective at detecting and predicting environmental perturbation and in translating their disciplines into understandable terms. However, we believe that scientists have been only partially effective in constructing a diagnosis for aquatic systems from existing data.

Therefore to parsimoniously define the effects from acidic atmospheric deposition, we attempted to (1) identify Canada's share of the global freshwater resources and (2) summarize the importance of Canada's freshwater industry. With this characterization of the resource, we then (3) identify the aquatic resource at risk from acidic atmospheric deposition, (4) outline the time course of fish species losses and (5) summarize direct and indirect evidence of effects from atmospheric deposition. Finally, we (6) evaluated the tenets collectively developed or extracted from bioassays, surveys, and experimental manipulation and (7) described their current use in models to assess/integrate the effects from acidic atmospheric deposition.

Freshwater Resources of Canada

Canada has close to half the total lake surface area in the world (Laycock 1987) and ranks third among nations of the world (after Brazil and the USSR) in quantity of riverflow (Healey and Wallace 1987). Yet, on a global basis, Canadian freshwater lakes, marshes, and rivers comprise only 15% of the world's surface freshwater supply (from data provided in Laycock 1987). In Canada, a general pattern of decreasing rainfall and increasing evaporation occurs from the NE to SW (Fisheries and Environment Canada 1978). There is a corresponding trend in lakes; thus in the SW, there are fewer, sometimes seasonally transient, lakes carrying a higher concentration of dissolved solids over the course of the rainfall/evaporation gradient. Brackish, salt lakes occur in the prairies and coastal regions. From measurements of lake areas in selected watersheds in eastern provinces (Fig. 1), it is apparent that Canada has many small (>55% are <10 ha) lakes. There also appears to be proportionately more small lakes in Quebec and Newfoundland than other eastern provinces. Consequently, despite the abundance of Canadian lakes, our pool of the freshwater lake volume of the world is limited.

The freshwater lake surface area of Canada, 755 180 km^2 (Table 1), forms 7.6% of our total nation's surface area, approximately 10^7 km^2 (Canada Year Book 1985). Canadian Shield lakes, those present on the relatively insoluble Precambrian bedrock areas of central and eastern Canada, are sensitive to acidic atmospheric deposition and many receive elevated sulphate loadings. On average, these lakes are moderate in size (mean = 240 ha), receive substantial amounts of rainfall (annual average 0.6–1.8 m from 30 yr of data (Fisheries and Environment Canada 1978)) and most have water renewal times <2 yr (D. S. Jeffries, Canada Centre for Inland Waters, Burlington, Ont., pers. comm.). Thin soils and high resistance of rocks to weathering make most of these Shield lakes clear, biologically unproductive, and long-lived because of low sedimentation rates. According to our best available estimates (Kelso et al. 1986), there are 167 355 km^2 (Table 1) of lake surface area (approximately 21% of Canada's total lake surface area) or 786 373 lakes (approximately 38% of Canada's total) in the region susceptible to acidic atmospheric deposition.

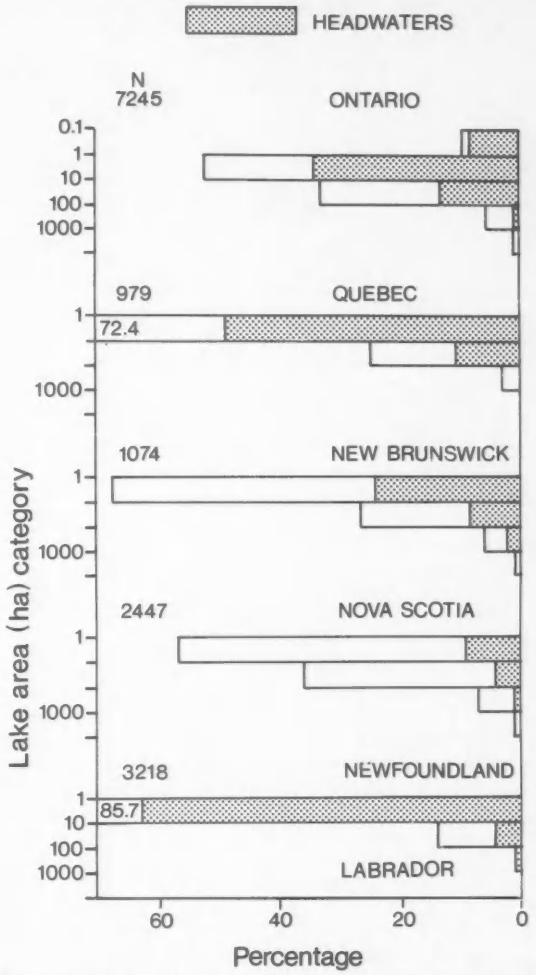

FIG. 1. Distribution of lake size (ha) by province in eastern Canada (from Kelso et al. (1986)).

General Characteristics of the Canadian Freshwater Fisheries

Many fish species are harvested from Canadian freshwaters in commercial and sport fisheries. Lakes on the southern portion of the Canaidan shield, in particular, frequently contain lake trout (*Salvelinus namaycush*) and brook trout (*Salvelinus fontinalis*) as dominant game fish species (Martin and Olver 1976; Johnson et al. 1977; Minns 1981; Legendre and Legendre 1984; Jeffries et al. 1988). Johnson et al. (1977) have also shown that in Ontario, four fish species: walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), lake trout, and smallmouth bass (*Micropterus dolomieui*) dominate communities of interest to sport fishermen and resource managers. In spite of our accumulated knowledge of fish species distributions in eastern Canadian Shield lakes, most studies have been biased to over-represent sport and commercial species (Johnson et al. 1977; Martin and Olver 1976; Minns 1981), accessible lakes, and/or larger lakes.

TABLE 1. Land and freshwater areas (km^2), by province and territory of Canada, including lake and surface area in provinces receiving SO_4^{2-} deposition in excess of background levels.

Province or territory	Land (km^2)	Freshwater[a] (km^2)	Freshwater with loading >background[b] Area	No.
Newfoundland	371 960	34 030	16 395	208 062
Prince Edward Island	5 660	—	—	—
Nova Scotia	52 840	2 650	2 650	6 585
New Brunswick	72 090	1 350	1 344	3 596
Quebec	1 356 790	183 890	90 313	441 752
Ontario	891 190	177 390	56 653	126 278
Manitoba	548 360	101 590		
Saskatchewan	570 700	81 630		
Alberta	644 390	16 800		
British Columbia	929 730	18 070		
Yukon	473 970	4 480		
Northwest Territories	3 293 020	133 300		
	9 215 430	755 180	167 355	786 273

[a] Canada Year Book (1985).

[b] U.S./Canada Memorandum of Intent on Transboundary Air Pollution (1983). Approximate region receiving loading above background. Data are from Kelso et al. (1986).

TABLE 2. Landed catches by anglers (modified from DFO 1984) and commercial fishermen (modified from Regier 1987) including their calculated value.

	Angler Total Catch (thousands)	Commercial Landed Total Catch (t)
Artic char	42	81
Arctic grayling	339	—
Bass, total	10 387	1 086
Northern Pike	12 164	2 490
Yellow perch	27 730	6 526
Salmon, total	4 108	16
Trout, total	28 231	1 214
Walleye (plus sanger)	20 058	7 258
Whitefish	2 159	12 588
Smelt	28 654	11 426
Others[a]	19 772	11 612
Value (thousands of 1984 Canadian dollars)	1 111 225[b]	48 352[c]

[a] For anglers, this catch included several marine species not normally found in freshwaters and unidentified species. For commercial catches this category included burbot, suckers, catfish, carp, shad, and several unidentified species.

[b] Includes directly related expenditures of food and lodging, transportation, fishing gear, and fishing services (DFO 1984).

[c] Value is landed commercial value only (from Regier 1987).

A further bias is introduced by examining data from sport and commercial fishermen. However, these data are at least indicative of how the resource is being used and of the value placed on the fishery resource (Table 2). Anglers commonly harvest walleye, trout, yellow perch (*Perca flavescens*), and smelt; commercial fishermen primarily harvest whitefish, yellow perch, and smelt. Although the dollar values associated with the harvest are not comparable (commercial valuation is strictly the landed value; the value of the angler's harvest includes direct and indirect expenditures (Table 2)), the endemic freshwater fishes clearly provide a significant contribution to the rural sector of the Canadian economy. According to Regier (1987), if complete harvest and evaluation data existed, the total value for the freshwater fisheries (including recreational, commercial food, and domestic bait fisheries), would approximate 1% of Canada's GNP (in 1987, ≃$5 billion Canadian). By comparison, the direct market value of the Canadian marine fishery in 1985 amounted to almost $2 billion (Canada Year Book 1988). Nevertheless, this valuation of the freshwater fishery resource in relation to the national financial account does not adequately express the dependence of small communities upon the resource. While it is possible to assign an economic value to the freshwater fishery, we cannot account for the social importance of the resource to rural communities and user groups.

The Aquatic Resource at Risk

Extensive analyses of lake surveys in eastern Canada are provided by Kelso et al. (1986) (biological and chemical data from approximately 1000 lakes) and Jeffries et al. (1986) (chemical data from approximately 5700 lakes). These data are considered representative of the lakes south of 52°N and east of the Ontario/Manitoba border (Kelso and Minns 1982; Kelso et al. 1986; Jeffries et al. 1986); i.e. the region generally accepted to be at risk from acidic atmospheric deposition. No significant differences exist (paired *t*-tests; $P<0.05$) between the two estimates (Kelso et al. 1986; Jeffries et al. 1986) of lakes in pH and alkalinity classes (Table 3). Assessments of acidic or sensitive (acid neutralizing capacity usually <100 $\mu eq \cdot L^{-1}$) lakes, however, do not necessarily imply that lakes have been acidified or will become acidic. The inference that lakes have been acidified from atmospheric deposition results from evaluation of the distribution of acidic lakes relative to SO_4^{2-} deposition and their ion balances. Rather, the syntheses of Kelso and Minns (1982); Kelso et al. (1986); Smith et al. (1986); Jeffries et al. (1986); and Underwood et al. (1986) identify vulnerable lakes and/or regions.

Assessments of lake status are incomplete for western or northern Canada; however, deposition, although normally <10, can exceed 20 $kg \cdot ha^{-1} \cdot yr^{-1}$ (wet sulphate) (Anonymous 1988). Hesslein (1979); Liaw and Atton (1980); and Shewchuck (1986) showed that lakes on the western Canadian Shield generally have pH's near neutrality and are well buffered. Acidic atmospheric deposition is lower than in eastern Canada; therefore, we suspect that the risk of acidification to lakes and streams is moderate in western Canada. Swain (1985), however, found lakes with pH<6 in southwestern, east-central and west-central B.C. Emitters in western Canada associated with industrial or mining centres can be expected to alter local water chemistry (vis-a-vis Sudbury, Wawa, Ontario).

Kelso et al. (1986) estimated (Table 1) that there were approximately 786 000 lakes in eastern Canada receiving deposition above background levels. We estimated from survey data that 391 000 lakes (≃50% of those receiving above background deposition) have an alkalinity <50 $\mu eq \cdot L^{-1}$. In addition, 15 619 lakes (2% of lakes receiving deposition above background levels) are estimated to be acidic (pH <4.7 cf Henriksen (1980)). We recognize that our estimate of low alkalinity lakes may be biased because we did not include lakes from western and northern Canada. Based on Kelso and Minns (1982); Kelso et al. (1986); and Jeffries et al. (1986), the status

TABLE 3. Estimates of lake resources and their chemical status of pH and alkalinity, by class and province.

	Ontario	Quebec	Newfoundland/ Labrador	New Brunswick	Nova Scotia	Total
Total No. of lakes[c]	126 278	441 752	208 062	3 596	6 585	786 273
Alkalinity <50[a] eq.L^{-1} (% of lakes)	32.2	52.0	54.2	47.8	93.3	
Alkalinity <40[b] (%)	22	55	58	51	93	
pH < 6[a] (%)	23	16	30	35	74	
pH < 6[b] (%)	19	30	34	36	83	
pH < 4.7[a] (%)	1.6	1.4	1.8	15.4	47.3	
pH < 5[b] (%)	3.1	3	2	7	39	
No. of lakes with alkalinity < 50 eq.L^{-1}	40 662[a]	229 711	112 770	1 718	6 144	391 005
No. of lakes with pH < 4.7[d]	2 020[a]	6 186	3 745	554	3 115	15 619

[a] Kelso et al. 1986
[b] Jeffries et al. 1986.
[c] Lakes south of latitude 52, generally receiving > background SO_4^{2-} from U.S./Canada Memorandum of Intent on Transboundary Air Pollution (1983).
[d] After Henriksen (1980).

described above generally represent lake conditions of the 1980–84 period.

Clearly, there are regional differences in the number of lakes at risk. Nova Scotia contains the highest proportion of both low alkalinity and acidic lakes. Variation in the SO_4^{2-} content of lakes approximated gradients in wet SO_4 deposition (Jeffries et al. 1986; Kelso et al. 1986). Naturally occurring organic acids do not appear to play a dominant role in the acidification of eastern Canadian lakes (Jeffries et al. 1986). If acidic lakes were primarily related to the presence of organic acids (i.e. lakes were naturally acidic) one would expect low alkalinity lakes to be associated with high organic acids. Jeffries et al. (1986) found that this was generally not the case. With the exception of northeastern Ontario (Sudbury and vicinity), low alkalinity lakes were spread across the range in concentration of organic acids. In northeastern Ontario, acidic lakes were usually clear with low concentrations of organic acids while elsewhere in eastern Canada, acidic lakes were often highly coloured.

Fishery Resource Impacts

Minns and Kelso (1986) used data from Kelso et al. (1986) to estimate the potential socioeconomic impact of acidification on the freshwater sport fishery. In eastern Canada, 3.7 million anglers spend in excess of $1 billion (Table 2 and DFO (1984)) in direct expenditures and in excess of $1.7 billion in indirect expenditures annually (DFO 1984). Minns and Kelso (1986), estimated that lakes with alkalinity <50 $\mu eq \cdot L^{-1}$ would contribute $576.6 million to the total annual expenditure by anglers. Assuming acidic lakes could contribute in a similar fashion if they supported a viable fishery, the estimated 15 000 acidic lakes (Table 3) represent a value of $53 million per year.

Most of the documented decrease in salmon production has occurred in Nova Scotia (Farmer et al. 1980; Watt 1981, 1986). According to Watt (1986), acidification in the southern upland region of Nova Scotia has reduced Atlantic salmon (*Salmo salar*) production from about 45 000 to 23 000 $fish \cdot yr^{-1}$. Assuming losses in Atlantic salmon production are limited to southern Nova Scotia, Watt (1986) estimated that streams too acidic to support Atlantic salmon would account for one-third of Nova Scotia's (3.2% of Canadian) Atlantic salmon. Brouard et al. (1982) identified spring pH depressions which may have an adverse impact on salmon rivers of Quebec's north shore of the Gulf of St. Lawrence. If salmon production in rivers elsewhere (e.g. Quebec's north shore and Newfoundland's south coast) are affected, then obviously a greater proportion of the Atlantic salmon fishery is at risk to acidic precipitation. The annual loss in revenue approximates $0.5 million for the loss of production in Nova Scotia's streams alone, based on a landed value of $100/fish (Watt 1986).

Assessment and projection of economic freshwater fishery impacts are only part of the atmospheric acidic deposition problem. The extrapolation of lake surveys to estimate the resource at risk (Kelso and Minns 1982; Kelso et al. 1986; Jeffries et al. 1986) and approximation of economic impact (Minns and Kelso 1986) do, however, provide a perspective to evaluate the seriousness of environmental alteration. Clearly, the freshwater fishery of Canada is important to the economy and its preservation is key to a nation highly dependent upon its natural resources. However, an economic yardstick seriously undervalues the full impact of resource damage.

Evidence of Relationships Between Fish Population Status and Aquatic Chemistry

Direct Evidence

A widely reported consequence of lake acidification due to acidic atmospheric deposition is the reduction or elimination of fish populations (Haines 1981; Harvey et al. 1981; Dillon et al 1984; and others). In Canada, the known population losses have been summarized by U.S./Canada Memorandum of Intent on Transboundary Air Pollution (1983); Harvey et al. (1981); Dillon et al. (1984); Harvey and Lee (1982); and Watt (1986).

The documented losses resulting from acidic atmospheric deposition are few, particularly cases where concomitant water chemistry (Fig. 2) data are available. Harvey and Lee (1982) suggest that the available data seriously under-represent the situation. The greatest losses appear to have occurred during the 1960's and early 1970's, but probably began (at least in

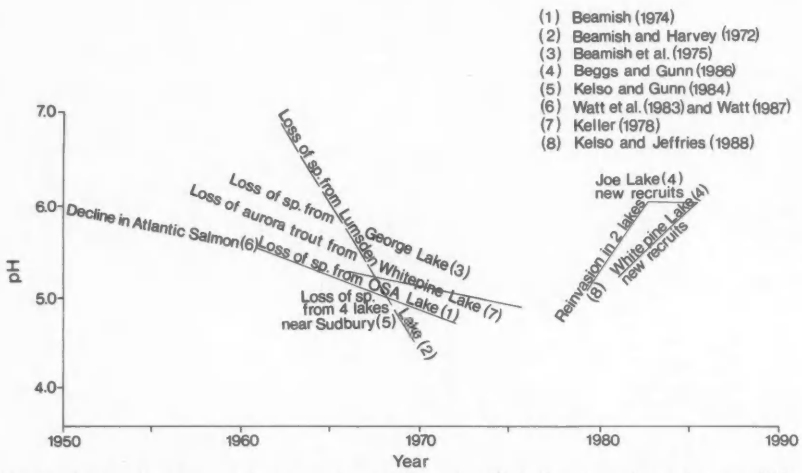

FIG. 2. Fish species response (line approximates change in pH) in Canadian lakes and rivers, 1950–present.

Nova Scotia (Watt et al. 1983)), in the mid-1950's. Support for these early losses is also provided by Keller (1978) who documented the decline of aurora trout (*Salvelinus fontinalis timagamiensis*) during the 1960's, and by Harvey and Lee (1982) who observed fish population losses near Sudbury during the 1960's and 1970's.

With the exception of Atlantic salmon, the documented losses of fish populations in Canada have occurred near Sudbury, Ontario. Somers and Harvey (1984) and Kerr (1982) suggested that fish stocks near Wawa, Ontario, may also have been lost. These lakes, however, were near a large local emission source and lake chemical changes were not documented. Collectively, the trend-through-time data strongly indicate a deterioration of environmental quality probably from the 1950's into the 1970's. Canadian attention was first focused upon the atmosphere as a source for contamination at Sudbury by researchers associated with the University of Toronto: (E. Gorham, A. G. Gordon, R. J. Beamish, and H.H. Harvey) in the late 1960's. Not surprisingly, the longest period of record, the most dramatic result, and continued research has centered in the Sudbury area. Other North American case histories, particularly the Adirondack region of New York State (Pfeiffer and Festa 1980; data summarized by Haines 1986; Haines and Baker 1986; and others) further exemplify the link between population success and water quality and confirm that greatest acidification occured in the 1960's and 1970's.

For most Canadian lakes, evidence indicates that damage due to acidification peaked in the late 1970's when researchers began to intensively study the issue. On the other hand, Dillon et al. (1984) documented a decrease in alkalinity and pH in Plastic Lake, Ontario. Because of limited data for the decades of major acidification (e.g. of references used for this paper, 2% were published in the 1960's, 25% in the 1970's, and 73% since 1980), we can only attempt reconstruction. Building case histories from anecdotal data, paleoecology (Johnson and McNeil 1988; Johnson et al. 1990) or deductions of likely changes in chemistry and fish communities (Minns et al. 1990) help establish the magnitude of change in water quality and its subsequent impact on fish communities. Recently, recruitment has resumed (Fig. 2) for at least some brook trout and lake trout populations (Beggs et al. 1985; Beggs and Gunn 1986) near Sudbury. Kelso and Jeffries (1988) also found evidence of reoccupation (reinvasion as opposed to recruitment resumption) by white sucker in two lakes ~350 km from Sudbury. Repopulation of these lakes was commensurate with improvement of water quality to pH's >5.0 in the early 1980's. Unfortunately we can reconstruct the degree of lake acidification with only uncertain accuracy. Consequently, establishing rehabilitation goals will be difficult.

Indirect Evidence

Many of the lake surveys in Canada were initiated to provide a basis for estimating the extent of the resource at risk or to describe current status of fish populations. The data base generated by these surveys has been used to assess relationships between fish community structure (distribution, number of species, diversity) or population characteristics (abundance, biomass, growth, or condition) and habitat. However, the empirical relationships can not directly link cause (i.e. acidification) with effect (e.g. reduced species diversity). The lake surveys also suffer from a bias towards:

(1) small/headwater systems (e.g. Kelso et al. 1986; Kelso and Gunn 1984),
(2) those with certain fish species (Beggs et al. 1985 and unpubl. data; Minns 1985; Beggs and Gunn 1986),
(3) those more likely to support game fishes (Wales and Beggs 1986),
(4) those with low (or high) pH (Frenette et al. 1986; Trippel and Harvey 1987), or
(5) unknown factors (Smith et al. 1986).

Despite biases, surveys have often produced results leading to development of testable hypotheses (Table 4). Published evidence indicates that:

(1) Species no. or species diversity are almost always positively correlated with pH (Kelso et al. 1982, 1986; Smith et al. 1986; Frenette et al. 1986).
(2) Many fish species are excluded from lakes at pH's unique to that species (Rahel 1985; Wales and Beggs 1986; Beggs and Gunn 1986; Beggs et al. 1985).

TABLE 4. Population responses inferred form recent biological surveys of Canadian Lakes. Catch-per-unit-effort (CUE) is assumed to reflect abundance.

Population parameter	Response	Source
Number of fish sp.	— decreased, also affected by lake size	Kelso et al. (1986)
	— decreased	Smith et al. (1986)
Diversity in fish community	— decreased	Frenette et al. (1986)
Abundance of fish	— CUE lower (most strongly influenced by lake size followed by pH)	Kelso and Gunn (1984)
	— CUE of lake trout was reduced at low pH	Beggs et al. (1985)
	— biomass strongly influenced by lake morphometry in a watershed	Kelso (1985)
	— no pH oriented trend	Smith et al. (1986)
	CUE of brook trout lower at lower pH	Frenette et al. (1986)
	— regional response (i.e. some areas CUE lower at low pH, not all areas)	Kelso et al. (1986)
	— white sucker abundance lower in low pH lakes	Trippel and Harvey (1987)
Fish distribution	— sp. distribution limited by pH	Wales and Beggs and (1986)
	— cyprinid sp. discriminated on basis of watershed characteristics and pH, alkalinity and Ca^{2+}	Bendell and McNicol (1987)
	— threshold identified for brook trout and lake trout	Beggs and Gunn (1986)
Condition factor (K) and growth	— inconsistent relation with pH	Kelso et al. (1986)
	— may increase/decrease at lower pH	summarized by Harvey (1982)
	— brook trout condition better at low pH	Frenette et al. (1986)
	— white sucker growth negatively correlated with pH (other factors also involved)	Trippel and Harvey (1987)

(3) Fish abundance is often positively correlated with pH (Kelso and Gunn 1984; Beggs et al. 1985; Frenette et al. 1986; Kelso et al. 1986; Trippel and Harvey 1987).
(4) Growth or condition ($K = W/L^3$) may or may not be correlated with pH.

While these studies have not demonstrated changes in fish community status or well-being over time, synoptic surveys have:

(1) focused on regions removed from Sudbury,
(2) identified lakes of low pH with fish communities having characteristics considerably different from those at higher pH's,
(3) yielded hypotheses amenable to testing in situations where variables can be controlled,
(4) provided empirical relationships that permit interpretation of conditions on a broader basis, and
(5) furthered the understanding of biological processes governing community status and well-being.

Survey data supports the hypotheses that lake acidification reduces or impairs fish communities, and has affected regions beyond the local influences of Sudbury.

Hypothesis Testing

The experimental acidification carried out at the Experimental Lakes Area (ELA) helps to resolve the sometimes conflicting results (Table 4) from studies in natural systems. At ELA, the whole lake acid addition to L223 commenced in 1976 (Schindler et al. 1985). Epilimnetic pH was gradually lowered from 6.5 to 5.1 between 1976 and 1981 and held near pH 5 from 1981–83. The manipulation of L223 does not replicate natural acidification of a lake because acid was added directly to the lake surface, the rate of acidification was accelerated, there was no spring episodic depression in pH and there was no mobilization of metals from the watershed. In spite of these differences, comparison of results from L223 with inferences from surveys (Table 5) has produced remarkable agreement in several areas. Expected responses, by fish in L223, inferred from theory and surveys, has been partially assessed previously (Mills et al. 1987).

There is particularly good agreement between the thresholds for successful recruitment observed for lake trout, fathead minnow (*Pimephales promelas*), white sucker (*Catostomus commersoni*) and pearl dace (*Semotilus margarita*) in L223 and those deduced from lake surveys. This agreement indicates that: (1) recruitment thresholds deduced from lake surveys are real and probably attributable solely to pH, and (2) fish species thresholds may be identifiable by appropriate laboratory testing. As a result, the descriptions of fish species distributions as related to pH or lake acidification (Beggs and Gunn 1986; Wales and Beggs 1986; Rahel 1985; and others) are reasonable. This approach should be applicable to other species, provided appropriate precautions in interpreting data (see Rahel 1985) are taken.

Some researchers have suggested that lake acidification should negatively influence fish abundance (Frenette et al. 1986; Beggs and Gunn 1986). Kelso and Gunn (1984); Kelso (1985); and Kelso et al. (1986) indicated that fish abundance, biomass, and production was most strongly related to lake morphometry and/or productivity, and that pH had a lesser influence on biomass and production. Data from ELA indicated that abundance and growth changed during the acidification, but

TABLE 5. A comparison between the response observed in L223, a lake acidified with H_2SO_4 addition, to the results inferred from surveys summarized in Table 4. Date for ELA from Mills (1984); Schindler et al. (1985); and Mills et al. (1987).

Population parameter	Response in L223 to acidification	Relation to survey result or "expected"
Number of fish sp.	— loss of two species (fathead minnow at pH 5.6 and slimy sculpin at pH 5.0) — increase of rare species beginning at pH 5.9	— not straightforward. Survey (empirical) approach likely overestimates the loss.
Diversity in fish community	— decrease, but not large change	— not good agreement, ELA data indicates that changes occur late in the acidification process.
Abundance of fish	— declines in fathead minnow, slimy sculpin — increase in pearl dace, lake trout, and white sucker (early stages) until recruitment failure, and then abundance declined	— uncertain relationship, ELA data indicates that survey catch data difficult to interpret. Supports the inconsistency of the survey result (response partly dependent on stage of acidification) and the need for examination of other factors (lake morphometry, productivity).
Fish distribution	— recruitment failure of fathead minnow, pearl dace, lake trout, white sucker and slimy sculpin	— good agreement with threshold identified in survey data analysis. Thresholds identified for fish at ELA marginally higher than inferred from survey data.
Condition factor (K) and growth	— condition decreased for lake trout, no apparent change for white sucker. Growth in length first increased for lake trout then decreased. Growth increased for white sucker.	— supports the divergent results reported from variety of studies. Response appears to result from restructuring in the food web, a lake specific response.

that the response differed among species. Abundance of some species (pearl dace) increased and, as a result, lake biomass (and perhaps fish flesh production) did not appear to decline in response to acidification. Schindler et al. (1985) also found that phytoplankton production and chlorophyll remained constant or increased slightly during acidification of L223. While there may be a tendency toward stability of community biomass, community composition and species contribution to fish flesh production in a lake can change dramatically in response to acidification.

During the acidification process, several divergent responses may occur: the number of fish species in a lake may/may not decline, growth may increase (white sucker in L223) or decrease (lake trout growth first increased then declined later in the acidification process), abundance may increase (pearl dace) or decrease (fathead minnows become extinct). The magnitude and direction of the response is likely influenced by the ability of species to invade, the resiliency of the endemic community and the plasticity of native and invading species. Fortunately, different experimental approaches have permitted a better appreciation of fish response to acidification. The disappearance of sensitive species provide our best biological early warning system. The fathead minnow may be the acidification equivalent to the miners canary. The determination of other fish population measurements (e.g. number of species, diversity, abundance, and growth) require considerable expenditure of effort and these response(s) may vary.

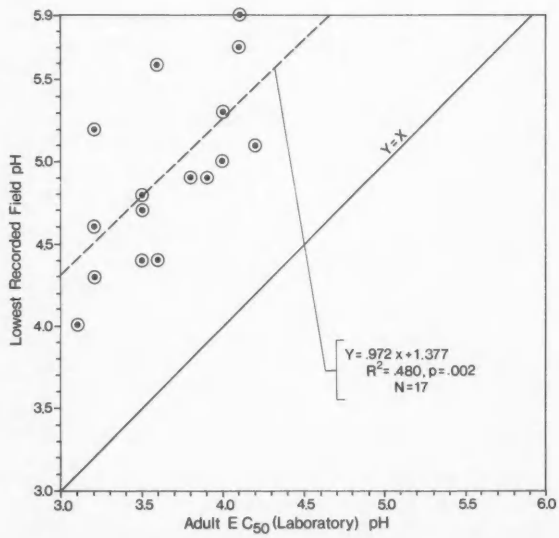

FIG. 3. Relation between lowest recorded pH in natural systems and laboratory EC_{50} for 17 fish species.

TABLE 6. Thresholds of pH for life stages of five species of fish in laboratory toxicity tests (LC_{50} in situ bioassays in natural systems, and avoidance data.

	Laboratory			Field				
Species	Adult Lc_{50}	Ecg Lc_{50}	Larval Lc_{50}	In situ survival LC_{50}	Alevin emergence	Reproductive threshold	Survey threshold	Avoidance
Book trout	3.5[2,8,17,30] (3.2–3.6)	4.4[12,37] (4.2–4.5)	4.3[2,19,37,38] (4.0–4.4)	Egg-Sacfry: 5.0[20] Fry: 4.9[4,12,20,] (4.8–5.2) Y.O.Y.: 4.9[20]	50% at 6.3[12] 1% at 5.5[12]	4.8[1,4,10,32] (4.5–5.0)	5.0[4,6]	Alevins: <5.0[13] Juveniles: 5.0–5.5[29] Spawning: <5.0[21]
Lake trout			4.3[19,23] (<4.0–4.7)	Egg-Sacfry: 0% < 4.9[7,20] Fry: 4.8[12,1,20] (4.6–5.0) Y.O.Y.: 0% at 4.6[12] < 5.3[3,20] Yearling: 5.8 <LC_{50}<6.6[1]	66% at 6.3[12] 2% at 5.5[12]	5.5[3,6,8,31] (5.4–5.6)	5.1[3,6] (5.0—5.2)	
Rainbow trout	4.3[12,26] Fingerling: 4.5[22,26] (4.3–4.5)	4.8[9]	4.2[9] (4.1–4.3)	50% hatch 5.9[11] Yolksac larvae: 5.7[18]	61% at 6.2–7.8 13% at 5.6–8.5 <0.1% at 5.2[11]		5.2[10,15] (4.9–5.5)	
Smallmouth bass	Y.O.Y. (overwintering): 4.9[36]	>90% hatch at >4.5[36]	5.0[16]	Juvenile: 5.0[4,14] (4.8–5.2) Y.O.Y. over-wintering: 4.8[4] Y.O.Y. over-wintering: 100% mortality at 4.9–5.8[27]		5.4[3,14] (5.0–6.0)	5.2[6,15,39] (5.0–5.5)	
Atlantic salmon		4.1[7,8] (3.9–4.5)	4.3[8]	Egg: 50% hatch at 4.7[24] Fry: 50% survival at 5.2[25] Smolts: 100% mortality at 5.0[35]		4.5[8] (inferred)	5.0[38]	

[1]Baker and Schofield (1980); [2]Baker and Schofield (1982); [3]Beamish (1974); [4]Beggs et al. (1985); [5]Beggs et al. (1985); [6]Beggs and Gunn (1986); [7]Carrick (1979); [8]Daye and Garside (1975); [9]Graham and Wood (1981); [10]Grande et al. (1978); [11]Gunn and Keller (1980); [12]Gunn and Keller (1981); [13]Gunn and Noakes (1986); [14]Gunn in Matuszek (1987); [15]Harvey (1979); [16]Holtze in Matuszek (1987); [17]Howells (1984); [18]Hulsman et al. (1983); [19]Hutchinson et al. (1985); [20]Johnson et al. (1987); [21]Johnson and Webster (1977); [22]Kwain (1975); [23]Kwain in Beggs et al. (1985); [24]Lacroix (1985); [25]Lacroix et al. (1985); [26]Lloyd and Jordan (1964); [27]Matusek (1987); [28]Mills (1984); [29]Pedder and Maly (1986); [30]Robinson et al. (1976); [31]Schindler et al. (1985); [32]Schofield (1976); [33]Schofield and Trojnar (1980); [34]Schuter in Matuszek (1987); [35]Skogheim and Roseland (1986); [36]Snucins in Matuszek (1987); [37]Swarts et al. (1978); [38]Trojnar (1977); [39]Wiener et al. (1984).

Bioassays in Evaluation of Lake Acidification Effects

Laboratory and in situ bioassays have been used to evaluate biological responses to acidification. The advantages of bioassays are their low cost and short duration. Many have tacitly assumed that they accurately reflect natural responses. Van Winkle et al. (1986) and Sadler (1983) proposed a framework to link laboratory and in situ population responses. Bioassays have been generally effective at screening sensitivity to toxicants. What has often been lacking is an understanding of their applicability to natural systems. We attempted to determine the consistency of the response measured by bioassay and observed in natural systems from data provided in the literature. Available reviews of toxic responses of fish to acid and metals (From 1980; Spry et al. 1981; Hofman 1987) essentially tabulate responses in bioassay experiments.

We matched the laboratory LC_{50} (for adults from bioassays over a range in time frames and a variety of test media) with the lowest recorded occurrence of that species in natural systems (Fig. 3) to evaluate compatibility of the two tolerance estimates. Both estimates were available for 17 species. Differences in species sensitivities were apparent and expected. However, the constant difference between the LC_{50} and the lowest pH at which that species occurred in lakes and/or streams ($r = 0.69$, $P = 0.002$) suggests an interesting underlying process. The derived regression (logarithmic) has a 1:1 relation between natural occurrence and the LC_{50}, offset by approximately 1.4 pH units. The lowest pH of species occurrence usually coincided with an apparent failure to reproduce. Thus, the inference is that species sensitivity applies, generally, to all life stages. If this hypothesis is correct, then testing an array of life stages in LC_{50} bioassays could be obviated. Figure 3 suggests, at least for $[H^+]$, that species have different toxic thresholds and that there is an additional, essentially constant, exacerbation in natural systems. Obviously, experimental testing of our hypothesis is required.

Evidence of stress in fish exposed to acidified water (with or without elevated levels of trace metals) has occurred through exposures of a variety of life stages in situ bioassays. The species for which these data were available, was limited (Table 6). In the in situ exposures, mortality was usually linked primarily to elevated concentrations of $[H^+]$ although trace metals (particularly aluminum), have been implicated. From these data, it appeared that early life history stages were the most sensitive. For brook trout, lake trout, smallmouth bass, and Atlantic salmon the field LC_{50} for eggs, sac fry, and larvae approximated the threshold for existence of these species in natural systems. However, none of the laboratory test data (an exception being the 7-d LC_{50} for smallmouth bass) approximated the threshold observed in natural systems. If our hypothesis that laboratory adult LC_{50}'s approximate the relative sensitivity of fish to H^+ (including trace metals elevated during the acidification process) can be generalized, then differential sensitivity among

TABLE 7. A comparison of features of models for integrated assessment of the emissions on aquatic biotic resources. Y = yes, N = no.

Model	Spatial scale[a]	*Elements*[b] E	D	A	*Damage* Biota	Other	*Biota criteria*[c] PA	R	BPY	*Groups* Fish	Other[d]	References
OMNR	L	N	Y	Y	Y				Y	Y	PZB	Marmorek et al. (1982)
HSM4	R	N	Y	Y	Y		Y		Y	Y		Minns et al. (1986)
ESSA-1	R	N	Y	Y	Y		Y		Y	Y		Minns et al. (1986)
ESSA-2	R	Y	Y	Y	Y		Y	Y	Y	Y	7 taxa	Marmorek et al. (1990) Jones et al. (1990) Minns (1990)
RAINS	R	Y	Y	Y	N	Soils Forest						Alcamo et al. (1987)
DDM	R	Y	Y	Y	Y		Y			Y		Small and Sutton (1986) Rubin (1987)
WALES	L	N	Y	Y	Y		Y	Y		Y	B	Ormerod et al. (1988)
LAF	L	N	N	Y	Y		Y		Y	Y		Van Winkle et al. (1986)

[a]L = local, R = regional.
[b]E = emissions, D = deposition, A = acidification.
[c]PA = presence/absence, R = assemblage richness/composition, BPY = biomass, production yield, tropho-dynamics.
[d]P = phytoplankton, Z = zooplankton, B = benthos.

species could be determined for any toxicant easily and rapidly using adults (or any convenient life stage) in bioassays.

It is difficult to apply the extensive battery of bioassays directly to interpreting responses of fish communities to acidification. Comparison of bioassay results with responses of fish in natural systems suggests that $[H^+]$ is the dominant toxicant. Also, confirmatory evidence of differential sensitivity and susceptible life stages are produced from bioassays. But, once determined, extensive repetition is not required. In our view, it is the underlying precepts of bioassays (e.g. differential sensitivity among species and relationships between laboratory and "field" results) that should receive further experimentation.

Integration of Cause and Effect through Model Development

A variety of consistent patterns of acidic atmospheric deposition effects have been integrated into a model framework for aquatic systems. It was reasonable to seek a method to establish to what degree the effect was linked to the root cause i.e. emission of acidifying materials into the atmosphere. For freshwater resources, the assessment integration framework consisted of the sequence: emission → deposition → lake/stream acidification → biotic change (damage). An integrated assessment of the processes would require that the spatial patterns of each of the four elements could be estimated. To adequately reflect ecological impact, the spatial boundary of such an assessment should include all emissions, incorporate all the biotic damage and be capable of providing predictions of how change in one element will lead to changes in others (i.e. for a given change in emissions, what will be the change in the pattern and degree of biotic damage). The key elements exist: emissions have ben inventoried (U.S./Canada Memorandum of Intent on Transboundary Pollution 1983; Environmental Protection Service 1986; and many others), deposition has been estimated (e.g. models presented in U.S./Canada Memorandum of Intent on Transboundary Pollution 1983) or measured through monitoring networks (Atmospheric Environment Service, Environment Canada; Ontario Ministry of the Environment and others in Canada and the United States), evaluations of lake chemical status have been constructed (Kelso et al. 1986; Jeffries et al. 1986; Linthurst et al. 1986) and biotic damage has been reported.

For those models with a biotic damage element, we classified them (Table 7) by the biotic criteria employed. Few models addressed the complete integrated assessment framework. All models included the deposition and acidification elements; indeed, Henriksen, Birkenes, MAGIC, and ILWAS models (Reuss et al. 1986) focused exclusively on those elements. The OMNR model used a complex trophodynamic model for a number of fish species and other biotic groups in a small set of lakes. The WALES (Ormerod et al. 1988) model used regression and multivariate models to predict changes in fish life-history parameters and macroinvertebrate assemblage structure. The CM model (Small and Sutton 1986; Rubin 1987) provided a complete integration framework from emissions to the presence–absence of selected fish species. The LAF model linked field observations of presence–absence to detailed toxicological observations over the complete life-history of several fish species. The RAIN model for European resources has many elements of an integrated assessment but lacks an aquatic biota damage element.

The models HSM-H, ESSA-1, and DFO-ESSA represent a chain of models developed for the Canadian Department of Fisheries and Oceans to measure biotic damage on a regional basis. All three models estimated biotic damage but only DFO-ESSA included emissions to provide a completely integrated framework. The HSM-H and ESSA-1 models focused on predictions of fish yield with presence–absence of fish species playing a role in the assemblage allocation of yield (Minns et al. 1986). The DFO-ESSA model used an array of biotic damage measures including fish species presence–absence, species richness for several groups of aquatic biota, and regression models of fish biomass, production, and yield. Reckhow (1988) examined how presence–absence patterns might be used to measure biotic damage. Schindler et al. (unpubl. data) have demonstrated how pH-species richness patterns can be used to assess biotic damage.

Models which link deposition and lake chemistry levels are handicapped by the lack of preacidification data in Canada (par-

ticularly original lake sulphate levels) and the difficulty of estimating the proportion of acid which falls on the watershed and is neutralized. All the models are difficult to validate because both input deposition and chemistry of a set of lakes must change and be measured. Model difficulties are compounded by uncertainties in estimating acid deposition rates from measurements in sparsely-populated monitoring networks. In Canada, uncertainties result from not knowing the number and sizes of lakes in affected regions (this problem is being addressed currently by R. Helie, Department of the Environment, Ottawa, pers. comm.). Only the DFO-ESSA, DDM, and RAINS models deal with regional resources and explicitly link the emittors to the response in the terrestrial and/or aquatic ecosystem. The biological effects models are most highly developed for the prediction of species richness. Prediction of single species presence–absence patterns is determined by a wide array of factors (most have no connection with lake acidification) and the maximum obtainable probability of presence is often much less than 1. Predictive models of effects on fish biomass and production are constrained by our ability to understand factors underlying their control. The fish models are incomplete in that the data sets used often had a limited range in lake size and nutrient status both of which influence biomass and production.

The models now available have been built on empirical models derived from emission inventories, lake surveys, and field and laboratory experimentation. Doubtless, other integrated assessment models will emerge to provide a basis for measuring emission control targets against damage on a regional scale. Of the models available, those directed at evaluating biotic effect from acidification by estimating biomass, production, and yield receive limited support from available evidence (see Tables 4 and 5). On the other hand, models incorporating critical thresholds of occurrence and, to some extent, community structure receive more support.

Summation

Part of the inability of the research community to respond to the admonitions of both Wilk (1985) and Schindler (1987) has resulted, we think, from three major inadequacies. First, the obvious estimates of vital resource attributes, including the resource at risk, are often missing! We know little of lake sizes, their geographic distribution, and how regional geology has influenced basic characteristics such as lake size or depth. Consequently, it is difficult to translate effects observed at a limited number of sites into an understanding of regional impacts. Secondly, our understanding of regional ecology and the principles that govern distribution and community production are sorely limited. Finally, the interpretations of environmental impact have often resulted from translation of results from only one type of study e.g. surveys, into an evaluation of the local, regional, or global response. In short, we have often failed to evaluate adequately how biological communities respond to stresses.

Attempts at synthesizing the diversity of "effects" from acidic atmospheric deposition data have resulted in a host of literature reviews and a series of "syntheses" from both industry and scientists. Many of these syntheses have received vitriolic rebuttals from the group not performing the synthesis! If nothing else, we hope this paper will provoke reasoned assessments of our interpretations, integrations of diverse ecosystem responses to stress(es), and evaluations of environmentalists' efforts at focusing attention upon an issue threatening preservation of resources.

As with other toxicological issues, if a suspected risk to ecosystem success, human health, or aquatic productivity exists, we believe the only reasonable answer is reduction of the toxicant.

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A Critical Review of Recent Freshwater Periphyton Field Methods

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Aloi, J. E. 1990. A Critical Review of Recent Freshwater Periphyton Field Methods. Can. J. Fish. Aquat. Sci. 47: 656–670.

I review recently published research (1970–89) on freshwater periphyton, with emphasis on epilithon and epiphyton. Brushing syringe-samplers are recommended for sampling epilithon, due to their low cost, ease of use, and effective removal of periphyton from firm substrates. Methods for removing epiphyton include scraping, agitation, and chemical methods, and the choice of methods is influenced by morphology of the macrophyte. Artificial substrates for periphyton colonization (glass slides, styrofoam, clay tiles, and nutrient diffusing substrates) are also evaluated. Although the use of artificial substrates may decrease substrate heterogeneity and allow more complex experimental designs in studies of benthic herbivory, differences between the natural and artificial substrates may affect population size or behavior of herbivores. Methods for measuring primary productivity of periphyton (O_2 and ^{14}C methods) and recent advances in microelectrode technology that allow microscale measurements of productivity and several other parameters are discussed including key references for novice users. General recommendations include: (1) sampling periphyton on naturally occurring substrates rather than artificial substrates when measuring biomass, primary productivity or species composition; (2) using artificial substrates when experimental design dictates, but not ignoring their limitations; and (3) including accurate descriptions of methods to allow future comparisons between studies in different systems.

Notre étude est une synthèse des travaux récents (1970–89) sur le périphyton dulcicole, et notamment sur l'épilithon et l'épiphyton. Il est recommandé d'employer pour échantillonner l'épilithon des échantillonneurs à brosse et à seringue à cause de leur faible coût, de leur facilité d'utilisation et de leur efficacité pour prélever le périphyton sur des substrats durs. Le prélèvement de l'épiphyton se fait par raclage, par agitation et par méthode chimique, selon la morphologie des macrophytes. Nous examinons aussi l'emploi de substrats artificiels (plaques de verre, styromousse, carreaux d'argile et substrats diffusant des nutriants) qui sont colonisés par le périphyton. Bien que l'emploi de substrats artificiels réduise l'hétérogénéité des substrats et permette de concevoir des expériences plus complexes pour l'étude des herbivores benthiques, les différences entre les substrats naturels et artificiels peuvent influer sur l'effectif des populations ou le comportement des herbivores. Nous examinons les méthodes de mesure de la productivité primaire du périphyton (avec O_2 et ^{14}C) et les progrès accomplis dans le domaine des microélectrodes, qui permettent des micromesures de la productivité et de plusieurs autres paramètres, en donnant quelques références de base pour les utilisateurs novices. Nos principales recommandations sont les suivantes : (1) échantillonnage du périphyton sur des substrats naturels plutôt qu'artificiels pour mesurer la biomasse, la productivité primaire ou la composition spécifique; (2) emploi de substrats artificiels lorsque la conception de l'expérience l'exige, mais sans ignorer leurs limitations; (3) description précise des méthodes employées pour permettre dans l'avenir des comparaisons entre études menées sur des systèmes différents.

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I. Introduction: Definitions and Scope of Review

Recently, investigations of aquatic systems have included increasing numbers of studies of periphyton. The periphytic community is important in investigations of whole-system productivity (Cushing and Wolf 1984), food web interactions (Elwood and Nelson 1972; Cuker 1983), herbivory (see review by Gregory 1983), trophic status (Stevenson et al. 1985), and because of its stationary nature, in monitoring sources of pollution (Chessman 1985) or nutrients (Goldman and de Amezage 1975; Lowe et al. 1986). Unfortunately, lack of methodological standardization handicaps studies of periphyton community structure, biomass, and primary productivity (Rosemarin and Gelin 1978). Comparison of published results is difficult, if not impossible. In a recent symposium volume on periphyton, Sand-Jensen and Bohr (1983) stated that "development of standard methods, if possible, for sampling of periphytic communities on different substrata should be attempted. Particular attention should be directed to the efficiencies of different sampling methods." In the same volume, Slàdeckovà and Barica (1983) point out the need for a methodological "manual" which would serve as a guide for researchers who are unfamiliar with the area, as well as provide a critical review of existing methods. I intend this paper to fulfill that role.

No review exists that covers the recent developments in methods for periphyton research (e.g. in situ primary productivity chambers, nutrient diffusing substrates), yet adequately evaluates the efficacy of existing methods for different types of investigations. The manuals which are commonly referred to are often outdated, and describe limited methodology which

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may not be appropriate for experimental work (Weber 1973, APHA 1985). Other reviews have been restricted to evaluating the use of artificial substrates for periphyton growth (Slàdeckovà 1962; Austin et al. 1981). In this review, sampling methods for periphyton on naturally occurring substrates will be evaluated, and compared with sampling artificial substrates. In addition, use of naturally occurring and artificial substrates in investigations of benthic herbivory will be assessed.

In this review, the term periphyton will be defined as the microfloral community living upon the surfaces of submersed objects in water (Wetzel 1983). This definition does not include fungal, bacterial, protozoan and other animal components, which are included in the definition of *Aufwuchs*, although this distinction is not made by many authors (e.g. Weber 1973). Periphytic communities can be loosely divided into those associated with inorganic substrates and those associated with organic substrates. Using the terms most commonly found in recent literature, epilithon refers to periphyton on rock substrates, epipelon on mud or silt substrates, epipsammon on sand substrates, and epiphyton on the submersed portions of aquatic macrophytes. In this review, discussion will be limited generally to freshwater epilithic and epiphytic communities, except where methods developed for marine systems are appropriately applied to freshwater systems. For more information on sampling epipelic communities, the reader is referred to papers by, and references contained in, Jenkerson and Hickman (1983a) and Stevenson et al. (1985). In addition, laboratory methods for chlorophyll extraction and estimation (see Reimann 1982; Marker et al. 1986), ATP extraction (see Stephens 1987) and the statistical techniques associated with algal enumeration and diversity indices (see Peet 1974; Stevenson and Lowe 1986) will not be discussed.

II. Sampling Periphyton on Natural Substrates

Epilithon

The earliest studies of periphyton were merely qualitative surveys of species distributions, and papers of this kind are still published (Dickman and Krelina 1975; Lampkin and Sommerfeld 1982; Kingston et al. 1983; Rushforth et al. 1986). Frequently, papers contained only vague descriptions of the methods. Morgan (1987) stated that periphyton samples were "collected" bimonthly, but never described specifically how the samples were collected. Similarly, Tett et al. (1978); O'Quinn and Sullivan (1983); and Jönsson (1987) reported that periphyton was collected, but did not describe the methods for removal of epilithon in sufficient detail for other investigators to repeat it.

The development of quantitative methods in periphyton sampling has facilitated quantitative periphyton measurements. Sampling methods range from simply scraping periphyton from rock substrates to using rather complicated periphyton samplers.

Scraping

Most investigators sampled epilithon by scraping a known area of the rock surface with a scalpel (Moore 1974, 1977; Power and Matthews 1983) or brush (Blinn et al. 1980; Ennis and Albright 1982). A timed scraping technique may standardize the efficiency of scraping for one investigator (Ward 1974; Cline et al. 1982) but this method suffers from high inter-investigator variability. The efficiency of these sampling methods was not well documented, although Moore (1974) stated that scraping rocks with a scalpel blade was 90% efficient for measurements of chlorophyll or biomass, but may underestimate species diversity, since many adnate species may be missed. However, scraping with a blade is only appropriate for smooth surfaced rocks. For rocks with macroscopic pits and crevices, a brushing method is recommended. To avoid missing tightly attached species, Lay and Ward (1987) submerged the entire rock substrate in organic solvents for chlorophyll determination.

Syringe samplers

The periphyton sampler developed by Stockner and Armstrong (1971) has been widely used and modified. Their original sampler consisted of a plastic 50-cc syringe with a toothbrush on the end of the plunger which removed periphyton from a 5.7 cm^2 area. This type of sampler is relatively simple to construct from materials which are widely available. The development of this simple sampler was very important as it allowed replicate sampling without removal of the rock substrate from the water. The brushing mechanism also made it very efficient in removing periphyton from smooth and rough surfaced rocks.

Similar samplers, which consisted of a syringe or tube sealed to the rock with rubber or neoprene, have been used by others (Tuchman and Stevenson 1980; Hornick et al. 1981; Hill and Webster 1982; Robinson and Minshall 1986; Robinson and Rushforth 1987). Typically, the rock and sampler were both removed from the body of water and the periphyton removed with a brush and pipette. This was a simple method for use in streams or the eulittoral zone of lakes, but has obvious limitations for sampling large rocks, bedrock, or deeply submersed substrates.

Hamala et al. (1981) developed a rather involved portable pumping sampler which may be used when the substrate cannot be removed from the water. Unfortunately, this was still limited to fairly shallow water (<30 cm). A similar sampler was used by Cuker (1983), consisting of a long tube put into the water and sealed to the substrate. The periphyton delineated by the tube was brushed from the rock with an electric drill fitted with a test tube brush. The slurry was removed with a Pasteur pipette.

The single-syringe sampler developed by Stockner and Armstrong (1971) was not effective in streams, or when sampling heavy growths of periphyton. Periphyton which was not actually entangled in the brush bristles would be swept away by the current or fall out of the sampler when lifted from the substrate to be corked. Modifications by Perkins and Kaplan (1978) and Loeb (1981) alleviated this problem with the addition of a second syringe which collected the loosened periphyton (Fig. 1a). This sampler was made from two 60-mL plastic disposable syringes and a toothbrush and was quite inexpensive, easily constructed, and allowed sampling of many different habitats and depths with sufficient replication (Cattaneo 1987; Hart 1987).

Field testing of this two-syringe sampler by one investigator yielded sample loss and incomplete flushing of detached epilithic material (Flower 1985). Additionally, because the surrounding water was drawn into the sampler, the periphyton sample may have been contaminated by phytoplankton and surrounding loosely attached epilithon. Alternatively, Flower advocated a brushing sampler which used a flushing system with pressurized water. This complicated sampler, however, was labor intensive, and worked well only in shallow water (20–50 cm).

This author has used the modified Loeb (1981) sampler for over 7 yr in a variety of lotic and lentic investigations. The sampler efficiently removed periphyton from the substrate both

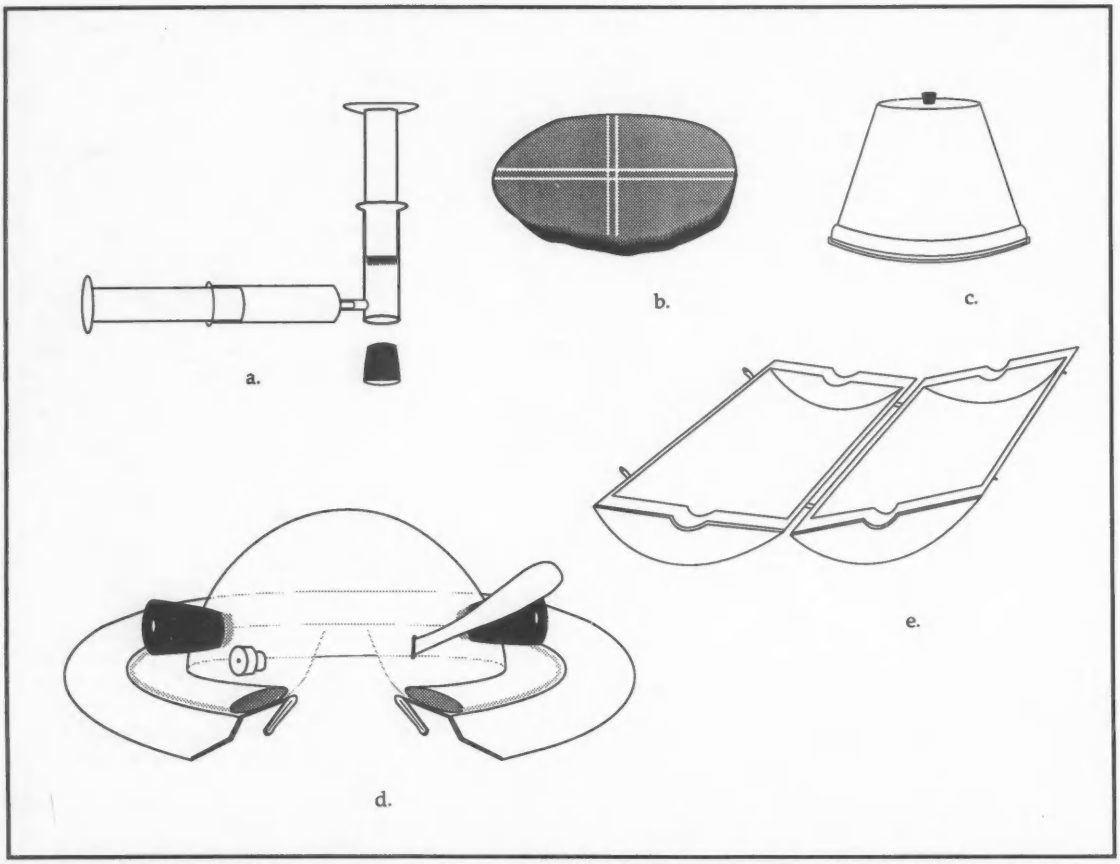

FIG. 1. (a) Two-syringe sampler for removing epilithon, consisting of two 60-cc syringes. The brushing syringe has a toothbrush attached to the end of the plunger. The collector syringe is attached near the base of the brushing syringe with plastic tubing (Loeb 1981). (b) Rock sectioned and glued together with silicon sealant for SEM analysis of center 1-cm^2 section (Keithan and Lowe 1985). (c) Nutrient diffusing substrate (clay flowerport) (Fairchild and Lowe 1984). (d) Cut-away view of incubation chamber for in situ epilithon primary productivity determinations. The chamber seals to the substrate with a double neoprene seal, and is weighted with a lead ring. ^{14}C is injected through the serum cap, and mixed by squeezing the pipette bulb. After the incubation, the two corks are removed and ^{14}C is flushed from the dome into a plastic waste container (Loeb 1981). Periphyton may then be sampled in situ with a brushing sampler, or by scraping after removal from the water. (e) Incubation chamber for in situ epiphyton primary productivity determinations. The two halves of the PVC chamber seal around the plant with neoprene, through which the ^{14}C is injected (Haines et al. 1987).

in shallow waters and at depths requiring SCUBA. No other published method could be used at great depths on rocks which are too large to be brought to the surface. The only critical limitation of the brushing sampler was the size of the rock; the sampler works well on rocks from boulder to cobble size, but small cobbles need to be held in place by a second person, as they tend to wobble during sampling. In addition, this sampler was used in conjunction with dome-shaped in situ productivity incubation chambers (see Section V). Although this sampler does indeed draw in a small amount of the surrounding water, the advantages of this method (cost, ease of use, efficiency) outweigh the limitations posed by Flower.

Bar-clamp sampler

Gale (1975) developed a bar-clamp sampler which had the advantage of preventing any loss of periphyton while removing the rock from the water. A clamp was tightened around the rock, and a sampling cup prevented the periphyton in a prescribed area from being disturbed while the rock was removed from the water. After removal from the water, periphyton from the sample area was cleaned with an ultrasonic dental cleaner. However, this method only works on relatively small rocks, and is more complicated to construct than most samplers.

Sampling macroscopic algae

Sampling of macroscopic algal species requires less involved methods. Müller (1978, 1983) sampled *Cladophora, Vaucheria*, and *Ulothrix* by cutting the filaments within a delineated area with scissors or forceps. Kay and Butler (1983) documented changes in macroscopic species over time using photography. Power and Matthews (1983); Power et al. (1985); and Power and Stewart (1987) estimated standing crop of periphyton in pools by recording dominant and subdominant algae (determined macroscopically), algal cover (sparse to 100%),

condition (senescent to fresh), and height (length) of the algal strands. Although these are subjective measures, in this study, height of algal strands was shown to be strongly correlated with ash-free dry weight (AFDW) per square centimetre.

Epiphyton

Quantification and identification of epiphyton generally necessitates removal of the epiphyton from the macrophytes. The methods of removal of epiphyton from macrophytes fall into three categories: scraping, agitation, and chemical methods.

Scraping

Epiphyton in removed by scraping when the morphology of the macrophyte permits: e.g. *Phragmites* (Roos et al. 1981; Riber et al. 1984; Meulemans and Roos 1985), *Glyceria* (Lodge 1986), or marine macroalgae (Medlin 1980). However, most freshwater macrophytes do not withstand scraping, or are finely divided, making complete removal of epiphyton difficult.

Agitation

The majority of studies involved shaking or stirring the plant to dislodge the epiphyton. Carignan and Kalff (1982) acknowledged the shaking did not remove the tightly attached epiphytes, but noted that scraping would remove some of the macrophyte biomass as well. Microscopic examination showed that shaking (20 s, 3 shakes/s) and rinsing eight times removed 85% of the diatom frustules (Jones and Adams 1982). Morin and Kimball (1983) reported 90% removal of epiphytes from *Myriophyllum heterophyllum* by stirring the plant in a beaker for 20–40 min with a magnetic stirrer. In an effort to standardize the force used to remove epiphytes, Gough and Woelkerling (1976) suggested the use of a modified paint shaker.

Chemical methods

Chemical methods are also available. The most commonly used method involved the addition of FAA (two parts formalin, 10 parts 95% ethyl alcohol, one part glacial acetic acid, seven parts water). This achieves periphyton removal by hydrolyzing polysaccharide mucilages of attached periphyton. Gough and Woelkerling (1976) reported that a 45-s agitation in FAA, followed by decantation, repeated five times assured almost complete removal of epiphytes (96.3–99.7% removal) on *Myriophyllum, Utricularia, Potamogeton pectinatus, Sphagnum,* and *Nuphar* petioles. When only diatoms are of concern, the entire plant may be chemically oxidized, leaving only cleaned diatom frustules (O'Quinn and Sullivan 1983).

Microscopy

Direct observations of epiphytes on macrophytes is possible, but only a low algal densities (Siver 1980; Carter 1982; Paterson and Wright 1986). Scanning electron microscopy (SEM), however, can be done by preparing the entire intact plant and attached epiphytes (Montfrans et al. 1982; on eelgrass; Paterson and Wright 1986, on *Elodea*). This method has the obvious advantage of allowing direct observation of the community structure of the intact epiphyton, but is very expensive and time consuming. SEM preparation and subsequent identification of diatoms and other species with siliceous or calcareous frustules or loricas is relatively easy, but preparation and identification of 'soft-bodied' algae is much more difficult.

Loosely versus tightly attached epiphyton

Some recent work has addressed the difference between loosely and tightly attached epiphyton (see discussion by Burkholder and Wetzel 1989). When a plant is removed from the water during the collecting process, the loosely attached epiphyton may be lost, and this loss is often ignored (Gons and van Keulen 1983; Rogers and Breen 1983). Jenkerson and Hickman (1983b); Kairesalo (1984), and Haines et al. (1987) devised special tubular samplers which enclosed the plants (reed stems), allowing them to be brought to the surface without losing the loosely attached epiphyton. Size limitations may make this technique unsuitable for large, finely divided plants, and differentiation between epiphyton and plankton is required.

It is evident, however, that the loosely attached epiphyton are an important component of the epiphytic community. Hill and Knight (1987) pointed out the importance of differentiating between the loose and adnate periphyton in grazing studies. In a study of mesotrophic Lake Memphremagog, the tightly attached community made up 70–80% of the total biomass during most months of the year, but only 20% during June (Cattaneo and Kalff 1979). Haines et al. (1987) separated the loosely and tightly attached epiphyton in one experiment and showed that the loss of the loosely attached epiphyton led to significant underestimations in both biomass and primary productivity. In sum, it is critical that sampling of epiphyton include the loosely attached species. Loss of this layer would decrease total biomass and productivity estimates, and likely alter the species composition.

III. Sampling Periphyton on Artificial Substrates

An artificial substrate has been defined by Cairns (1982) as a "device placed in an aquatic ecosystem to study colonization by indigenous organisms." Hentschel (1916) published the first research describing the use of artificial substrates (glass slides). Artificial substrates, particularly glass microscope slides, were the standard in periphyton research for many years after Hentschel's paper (Patrick 1967; Patrick and Roberts 1979). Slàdeckovà (1962) thoroughly reviewed the use of artificial substrates through 1962 (431 references). Slàdecek and Slàdeckovà (1964) also evaluated the use of artificial substrates, particularly glass microscope slides. In a recent review, Austin et al. (1981) described numerous artificial substrates, with observations on how they worked. Unfortunately, no information on the replicability of the substrates or comparison with the natural community was given.

The use of artificial substrates has been justified by researchers for a variety of reasons, most commonly to reduce the heterogeneity of the naturally occurring substrate (Schindler et al. 1973), or for a standard means of comparison between two habitats or sites with differing substrates (Stockner and Shortreed 1976). Other reasons include decreased cost of sampling, decreased disruption of the habitat, and decreased time to obtain a quantitative sample, since the surface area of the substrate is known (Lamberti and Resh 1985). Artificial substrates may also be used when naturally occurring firm substrate is absent (Hansmann and Phinney 1973).

The ideal artificial substrate has several characteristics. First, samples taken from the substrate must be precise; i.e. the coefficient of variation (CV) of the samples from the artificial substrates must be equal to or less than the CV of the samples from the naturally occurring substrate. Also, the colonization time required for the artificial substrate must be short enough to satisfy the design of the experiment, and the artificial substrate should be easily retrievable without sustaining loss. Also, if the experimental design assumes that the artificial substrate is a

substitute for the natural substrate, the periphytic community of the artificial substrate must accurately represent the community composition and abundance on the naturally occurring substrate (rock, plant, etc.). However, not all experiments require that this last requirement be fulfilled. For example, in a grazing experiment, a homogeneous substrate may be critical and resemblance to the natural community may not be essential.

Glass Slides, and Other Glass Substrates

Glass slides have been the most commonly used artificial substrate for periphyton colonization, particularly after the development and popularization of the Catherwood diatometer by Patrick et al. (1954). This sampler consisted of a holder for microscope slides buoyed by styrofoam floats. The diatometer is still in use in water quality monitoring, where the use of a standardized substrate is advantageous (Chessman 1985). Glass slides, in a variety of "customized" slide holders, continued to be used in studies of periphyton (Hunter 1980; Marcus 1980; Bamforth 1982). Many studies cited the need for a uniform surface in experimental work as the reason to use glass slides. Glass slides are also advantageous because they are inert, inexpensive, and periphyton may be easily removed by scraping.

The orientation of glass slides (horizontal versus vertical; parallel versus perpendicular to the current) has been variable. In my review of 25 randomly chosen recent studies employing glass slides, 13 used vertically oriented slides, four used horizontally oriented slides, and eight were comparison studies using both vertically and horizontally oriented substrates. Although vertically positioned slides are colonized more slowly, algal populations on both sides of the slides are quantitatively and qualitatively similar. Horizontal positioning resulted in a greater accumulation of biomass, but often with a great amount of settling and detritus (Bamforth 1982). When a heavy growth of periphyton developed on the upper side, the bottom became dominated by heterotrophic organisms, so usually only the top side was sampled (Brown and Austin 1971). If the objective of a study is to use the periphyton assemblage as a bioindicator of some physicochemical conditions, vertically positioned slides are recommended to decrease detrital accumulation and to encourage growth of attached periphyton species. Alternatively, if the slides need to be subjected to the same colonization and grazing by invertebrates as the naturally occurring horizontal rock surfaces, horizontal positioning is appropriate.

When glass slides are used in stream studies, they are generally placed vertically and parallel to the current (Oemke and Burton 1986). Munteanu and Maly (1981) positioned slides vertically, both parallel and perpendicular to the current and demonstrated that diatoms showed a marked preference for the leading edges of the slides parallel to the current. Evidence from their flow models of a liquid around a slide showed that this is an area of stagnation, and therefore a likely spot for initial diatom attachment. No similar patterns were seen on vertical slides perpendicular to the current.

Several studies measured the variation in periphyton biomass on glass slides, coverslips, and culture tubes. Meier et al. (1983) reported a lower CV for chlorophyll samples of periphyton on glass culture tubes compared with coverslips. In a similar study, Dilks and Meier (1981) reported that the CV for chlorophyll measurements between replicate glass coverslips was only 4%. Although their study only measured periphyton biomass on one type of substrate, they stated that their method reduced variability between replicates, when compared with values for periphyton accrual on replicate slides (20–25%) cited in Weitzel et al. (1979). In contrast, in a similar study, Weitzel et al. (1979) did find statistically significant differences (variation 0–100%) in both biomass and chlorophyll measurements on glass slides between replicated side-by-side samplers. In addition, within-sampler variation ranged from 20–30%, and was not related to slide position in the sampler.

Although many investigators have assumed that algal communities on glass substrates were identical to the naturally occurring epilithic or epiphytic communities, few studies have verified this. Luttenton and Rada (1986) stated that the community architecture of epiphytes on *Cladophora* was similar to that on glass slides in the Mississippi River, but didn't present any supporting evidence. Stockner and Armstrong (1971) found diatom communities on glass slides and rocks to have similar seasonal periodicity, but there were differences in species abundances and biomass. The majority of the comparative research has shown that the periphyton growing on glass substrates is significantly different from the natural assemblage in terms of biomass (Brown 1976; Loeb 1981), chlorophyll (Rosemarin and Gelin 1978), species composition (Brown 1976; Siver 1977), and primary productivity (Loeb 1981).

Other Artificial Substrates

Rocks, tiles, and bricks

Naturally occurring rock substrates which have been cleaned of periphyton have been used in a few studies (Horner and Welch 1981; Lock et al. 1984), often utilizing cut rocks, which facilitated sampling by providing a flat, homogeneous surface. Lay and Ward (1987) compared chlorophyll and algal cell numbers on cut rock slabs and naturally occurring rocks. They found substantial differences in community composition, with a greater abundance of *Achnanthes* on rock slabs, and more green algae on the naturally occurring rocks. They suggested that this was due to the relatively short (30 d) exposure period. It may also have been due to the different surface texture of the sawed slabs and the naturally occurring rocks. Blinn et al. (1980) compared three different introduced rock substrates; sandstone, limestone, and basalt, and found much greater standing crop after 1 wk on the sandstone, and suggested that this was due to differences in microsurface morphometry. However, after the first week, and for the following 4 wk, no significant differences were measured, indicating that substrate selection plays only a limited role in community development.

Although a few early studies used clay tiles as substrates for periphyton growth (Huntsinger and Maslin 1976), Tuchman and Stevenson (1980) popularized the use of clay tiles in a widely cited paper, and tiles are now as commonly used in periphyton studies as glass slides were 20 years earlier. Tuchman and Stevenson evaluated the utility of sterilized natural rock substrates and unglazed clay tiles. Their study showed that periphyton biomass measurements on tiles were more reproducible than on sterilized rock substrates. However, the sampling area for the tile was 57 times greater than the rock, thus it is possible that the decreased variability of samples from the tile was the result of reduction in the heterogeneity of algal distribution. Clay tiles are inexpensive, and easy to use but not necessarily similar to the natural substrate because they lack the surface irregularities of most rocks, but do lack the greater tendency of rocks to roll or flip over (Mulholland et al. 1986). Clay tiles may facilitate some experimental work because they may be easily used to line the bottom of experimental channels, and they provide the

units for sampling. Tiles may be elevated from the substrate (Jacoby 1987; Lamberti et al. 1987a), and may be used in small enclosure experiments (Lamberti et al. 1987b). Sampling of clay tiles is achieved either by scraping the entire tile (Steinman and McIntire 1986; Stewart 1987), or a smaller area delimited by a template (Lamberti and Resh 1985). Concrete bricks and slabs have also been used to simplify experimental manipulation and to minimize substrate complexity, particularly in herbivory studies (Kohler 1984; Williams and Moore 1985; Robinson and Minshall 1986; Vaughn 1986; Robinson and Rushforth 1987).

Because tiles are now commonly used in herbivory studies, it is important to evaluate the effectiveness of tiles as substitutes for the naturally occurring substrate for periphyton growth, as well as invertebrate colonization. In the only published study of this kind to date, Lamberti and Resh (1985) evaluated clay tiles, sterilized rocks, and naturally occurring rocks as substrates for colonization by bacteria, algae, and macroinvertebrates in a 5-mo study in a California creek. Substrates were sampled at monthly intervals for bacteria, chlorophyll, AFDW, and total invertebrates. Their results were mixed. Bacterial numbers, chlorophyll, and AFDW were significantly different between substrates after certain exposure periods. However, macroinvertebrate density and species richness were significantly different only after the 1-mo exposure period. In all cases, the mean CV for the tiles was not significantly different compared with the natural rocks with respect to macroinvertebrate abundance.

Styrofoam

Researchers using the Catherwood diatometer often observed more periphyton growing on the styrofoam float than the glass slides. This is probably due to the porous surface of the styrofoam, which provides a low flow refugia and increases colonization rates (Stevenson and Lowe 1986). Lowe (1972) used suspended styrofoam spheres as substrates. Since only diatoms were of interest in this study, sampling was facilitated by dissolving the entire sphere in xylene, settling and decanting to remove the xylene, and oxidizing the organic matter in H_2O_2. Flint et al. (1977); Bothwell (1985); and Perrin et al. (1987) used anchored styrofoam sheets as substrates for algal colonization and sampled the sheets using a cork borer. This author sampled the styrofoam substrates placed by Flint et al. (1977) 9 yr prior (J. E. Aloi, unpubl. data). Biomass was significantly lower than the naturally occurring epilithon in the sublittoral of Lake Tahoe. This demonstrates that in this instance, either herbivory (probably by crayfish) is different on the two substrates, or the mature periphyton takes a very long time to develop.

Suspended polyurethane foam substrates (squares or spheres) have been used by Kuhn et al. (1981) and Cairns et al. (1983). These substrates are easy to manipulate, but have several serious drawbacks. Because the foam forms an open latticework, heterotrophic organisms may be over-represented within the substrate. Also errors may be introduced by losses resulting from repeated rinsings and squeezings of the substrate during the sampling procedure. Paul et al. (1977) compared colonization of sycamore leaves and polyurethane foam in a river and a pond. They found that algae were the predominant invaders of foam in the river, but bacteria and fungi dominated on foam in the pond, as well as leaves in both habitats. Clearly, polyurethane foam substrates may be useful in comparative studies focusing on bioindicator organisms, but do not develop naturally occurring periphyton communities.

SEM tabs

Aluminum SEM tabs are commonly used in studies investigating periphyton community structure. Blinn et al. (1980) sampled periphyton on aluminum SEM tabs to investigate community structure and development, but sampled naturally occurring rocks for determination of algal biomass and species composition. There was no attempt to determine whether similar communities developed on the two substrates. Hoagland et al. (1982) also used two different substrates; glass slides for SEM analysis of community structure, and Plexiglas for algal enumeration. Korte and Blinn (1983) compared diatoms growing directly on aluminum SEM tabs, and on Plexiglas discs on top of the tabs. Although there were no differences in a pool habitat, diatoms were 1000× more common on Plexiglas in a riffle habitat. They speculated that this was due to the differential surface tensions of Plexiglas (low energy) and aluminum (high energy). They cited other studies which have shown that bacterial colonization is more rapid on low energy substrates, and this may enhance diatom colonization. Perhaps the most appropriate method to date was described in Keithan and Lowe (1985), in which the natural rock was sectioned by making a series of cuts, resulting in a 1-cm^2 section in the middle of the rock (Fig. 1b). The rock was then glued back together with silicon sealant, and after an appropriate exposure period, this center section was used for the SEM analysis. This may also be a useful technique to apply to studies employing clay tiles.

Suspended Substrates

The Catherwood diatometer was the first of many studies employing substrates suspended in the water column (Goldman and de Amezaga 1975; Herder-Brouwer 1975; Austin et al. 1981; Kuhn et al. 1981; Eloranta 1982; Hoagland et al. 1982; Roemer et al. 1984; Shortreed et al. 1984). In none of these studies was the rationale for suspending the substrates justified. Some researchers have justified the use of suspended substrates for logistical reasons; e.g. Welch et al. (1972) suspended Plexiglas substrates from a surface float in an estuary, which kept the substrates at a constant depth during tidal movement. However, Wetzel (1965) points out that most substrates for periphyton growth are benthic or macrophytic and that substrates occurring in open water are not significant in lake or stream systems.

Evans and Stockner (1972) sampled periphyton from navigational buoys in a survey of Lake Winnipeg. Although the sampling sites were in two rather isolated basins, samples from buoys in close proximity often had distinct species compositions, often dominated by entirely different algal divisions. This demonstrates another problem with suspended (and perhaps benthic) substrates: periphyton species on the substrates are often distinctly different from each other, perhaps due to the "founder" or island effect.

Lang and Austin (1984) and Austin et al. (1981) sampled vertical nylon lines to determine the depth distribution of algae. However, Rosemarin and Gelin (1978) point out that samples from suspended substrates do not necessarily represent the natural benthic community. Physical factors (water motion), chemical conditions (groundwater influx), and biological factors (grazing) are not identical at correspondent depths suspended in the pelagic zone and on the benthic substrate. This is an important consideration in herbivory studies. Several recent experiments have elevated artificial substrates to exclude grazers and compared this community with that on grazed substrates on the stream bed (Jacoby 1987; Lamberti et al. 1987a).

These elevated substrates are not only affected by the release of grazing pressure, but may experience greater turbulence or shearing as well as differences in nutrient or light regimes. The optimal experimental design would include both grazed and nongrazed substrates on the bottom, but also experiencing the same light, nutrient, and current regimes.

Exposure Periods

Exposure periods for substrates also varied, ranging from as little as 1 d to as long as 3 yr in papers cited herein. Researchers commonly standardized the exposure time at 2 wk, or 1 mo. The length of exposure was usually determined by water quality (longer exposure in less productive waters), water temperature, or the purpose of the investigation. Oemke and Burton (1986) suggested that variations in current velocity, nutrients, temperature, and light influence colonization rate and sequence, and therefore one standard exposure period is not applicable for all environments. For determination of an appropriate exposure period for each investigation, physical conditions must be considered, as well as the purpose of the investigation. Short exposure periods are appropriate for studies of colonization and community development (Roemer et al. 1984). A series of sequential samplings of the substrate are appropriate for time–course studies; e.g. the study by Elwood et al. (1981) on the effect of artificial phosphorus enrichment of a stream. If the artificial substrates are to be used as a substitute for sampling of the natural substrates, the exposure period must be long enough for the community on the artificial substrates to fully develop (Tuchman and Blinn 1979). The general consensus seems to indicate that a minimum of 1 mo may be required in most systems, with oligotrophic systems requiring even longer periods of time.

Choice of the appropriate exposure period may be particularly important in experiments involving grazing on periphyton communities that develop on artificial substrates. Incubation periods range from only 1 wk (Kesler 1981; Sumner and McIntire 1982) to 1.5 mo (Hunter 1980). Unfortunately, short exposure periods may result in a lack of distinction between successional changes of the periphyton and herbivore effects.

Artificial Substitutes for Plants

One of the earliest artificial substitutes for plant substrates consisted of Plexiglas slides, wrapped with tape (Allen 1971). This was an attempt to overcome the problem of contamination by macrophytic tissue in estimates of epiphyte biomass and primary productivity. More recent studies have used substrates more closely resembling plant morphology, but are employed for the same reason. Higashi et al. (1981) and Goldsborough et al. (1986) used plastic rods as a substitute for stems of emergent macrophytes. Goldsborough et al. found that the CV for samples taken from the rods (chlorophyll, primary productivity, and particulate phosphorus) compared favorably with other published data (20 citations) on artificial substrates, although they did not compare this with samples taken from the macrophyte stems. In a well planned study, Mason and Bryant (1975) did compare the standing crop of periphyton on dead *Typha* stems and glass rods. They measured an increased standing crop of periphyton on glass rods compared with dead *Typha* stems. Fewer chironomids were found on the glass rods, probably because it is more difficult for them to attach and burrow, and the reduction in herbivore biomass in turn may have affected periphyton biomass. Millie and Lowe (1983) also measured significantly different diatom standing crops on wooden dowels and plant stems (*Typha, Nymphaea*, and *Polygonum*).

Plastic flagging tape has been used by other researchers, e.g. Montfrans et al. (1982) and Lethbridge et al. (1988) as a substitute for seagrasses. Other experiments have used plastic aquarium plants, selected for their morphological similarity to indigenous plants (Cattaneo and Kalff 1979; Cattaneo 1983; Morin 1986). There is little agreement on the effectiveness of these artificial substitutes for plants. Shamess et al. (1985) sampled both plastic flagging and *Typha* stems, and found very different algal communities in two eutrophic Canadian lakes. Alternatively, Morin (1986) found that species composition of epiphyton on *Myriophyllum* and similar artificial plants was not significantly different in a soft water New England lake. However, biomass was lower on the artificial substrate, which was suggested to have been due to some algal biomass remaining on the *Myriophyllum* after sampling. Cattaneo and Kalff (1979) showed that the "Hygrophila" plastic aquarium plants on "stems" of flexible rubber tubing were a good mimic of *Potamogeton richardsonii*.

These differing results may be attributed to the similarity of the artificial substrate to the plant, or may be related to lake trophic level. Eminson and Moss (1980) suggest that with increasing eutrophication, the interactive role of macrophytes as periphyton substrates becomes less important. Therefore, artificial plants may be more effective substitutes in high nutrient environments. Artificial plants differ from real plants in other ways which may cause these differences; plants continue to grow, they may precipitate carbonate, and are usually more morphologically diverse than artificial substitutes (Gons 1982). Finally, grazers that burrow in macrophyte tissue will probably be absent from plastic plant substitutes, and their absence will most certainly affect periphyton biomass and species composition.

Nutrient Diffusing Substrates

Experimental demonstration of nutrient limitation of periphyton growth has been problematic. Unlike phytoplankton, which may show elevated chlorophyll and primary productivity in response to nutrient spikes in short-term microcosm and mesocosm experiments, periphyton rarely responds within the same time frame (J. E. Aloi, unpubl. data from Lake Tahoe and North Wisconsin lakes). Fairchild and Lowe (1984) and Fairchild et al. (1985) described a now classic method for in situ bioassays of nutrient limitation using nutrient diffusing substrates. The substrates (clay flowerpots or flowerpot saucers) were filled with agar and a nutrient solution, inverted and glued to petri dishes, and placed in the lake or stream (Fig. 1c). Their experiments showed that these substrates continued to diffuse nutrients in proportion to the internal concentrations for at least 3 wk. After an appropriate exposure period, the periphyton may be sampled by scraping with a knife or a brushing sampler. A similar nutrient diffusing substrate composed of agar-consolidated sand and nutrients in a petri dish is useful in sampling periphyton that grows on sandy bottoms (Pringle and Bowers 1984). The periphyton can be easily sampled with a cork borer. Currently, diffusing substrates are being tested which diffuse insecticides which prevent colonization by invertebrates. These may prove to be very useful in studies of herbivory on periphyton.

Pringle (1987) pointed out that nutrient diffusing substrates are a useful technique in determining nutrient limitation in

aquatic systems, but they are functionally different from water enrichment assays in which nutrients are added at a constant rate. Since whole-stream enrichment experiments tend to be pseudoreplicated and/or without controls, Peterson et al. (1983) developed an in situ flow-through nutrient enrichment technique. Banks of Plexiglas tubes enclosing racks of microscope slides were suspended from floats parallel to the current in a stream. Concentrated nutrients were added via siphons into the upstream end of the tubes. This experimental design indeed allowed a control and replicates, was flood resistant, and eliminated the need for elaborate channels, pumps, or electricity. In a similar streamside experiment, Stockner and Shortreed (1978) utilized troughs through which nutrients could be supplied to individual channels. Although the treatments in this experiment were not replicated, this system could easily be expanded.

Grimm and Fisher (1986) evaluated nutrient diffusing substrates (periphyton on clay pots) and stream water enrichment (periphyton on clay tiles), and found that nitrogen addition elevated chlorophyll levels and primary productivity in both experiments. Critical comparison between the responses to the two treatments is not possible, because they were not run concurrently (the experimental schedule ran between July and November including episodic flooding) and some treatments were pseudoreplicated. Pringle (1987) compared periphyton growth on nutrient diffusing substrates (consolidated sand–agar substrates) and nutrient enriched flow-through banks. Again, both treatments showed stimulation of growth, with both additive and synergistic effects of the two nutrient sources evident. It is evident that both methods of nutrient enrichment may be useful, choice of method depending on the experimental objectives.

IV. Quantitative Measurements of Periphyton Biomass Measurements

The most basic information about a periphytic community is a measurement of biomass. This may be done by measuring DW (dry weight), or more commonly AFDW (combusted in a muffle furnace), chlorophyll (extracted in a solvent), caloric content (measured in a bomb calorimeter), or carbon content (measured in a carbon-nitrogen analyzer). DW and AFDW measure not only algal mass, but also bacteria, invertebrates, and organic detritus. Measurements of chlorophyll are derived only from the algal fraction, but the ratio of algal chlorophyll to biomass varies among algal species, and contamination from detrital chlorophyllous pigments is a problem (Reimann 1982). Caloric content may be valuable information in a grazing study, and carbon content is useful in relating biomass to productivity.

AFDW is calculated as the difference between dry weight and the weight of the ash after combustion. However, the times and temperatures of drying or combustion have not been standardized. In a review of nine randomly selected papers, the time for drying (DW) ranged from 12–48 h, at temperatures of 60–105°C. Standard Methods for the Examination of Water and Wastewater (APHA 1985) recommends drying samples at 105°C for 24 h. Personal experience has indicated that samples should be dried at approximately 60°C until a constant weight is achieved as higher temperatures may result in a loss of some volatile organic compounds. Likewise, the reported times for combustion (AFDW) ranged from 1–4 h, at temperatures of 400–650°C. In many papers, no times were reported. One study reported that the sample was combusted at 400°C, rather than 550°C to avoid dehydroxylation of the clay fraction (Biggs 1987). APHA (1985) recommends combusting samples for 1 h at 500°C, then rewetting to restore the water of hydration to the clay fraction, then redried to a constant weight at 105°C. For sedimentary samples, Dean (1974) reports that a temperature of 550°C is optimal, since organics are not removed at lower temperatures, but carbonates are lost at higher temperatures. Therefore, adoption of 550°C for ashing samples is recommended, and rewetting and drying at 105°C if the sample has a high sediment content.

Periphyton Identification and Enumeration

Discussion of species identification, diversity indices, etc. will be left to other reviews (Peet 1974; Stevenson and Lowe 1986). Two good sources for lists of references for algal taxonomy are George (1976), for a listing of algal keys excluding seaweeds, and Stevenson and Lowe (1986), for a suggestion of the best general references.

The morphology of periphyton (e.g. motility, mode of attachment) has a direct bearing on their ecological characteristics. Lowe et al. (1986) suggested a classification by algal physiognomies: prostrate to stalked (taxa that may be either prostrate or stalked, e.g. *Achnanthes*, *Gomphonema*), "*Eunotia*" type, motile (nonstalk-forming biraphid diatoms), prostrate (nonstalk-forming monoraphid diatoms), filamentous and erect. Hoagland et al. (1982) also discussed the 3-D life-forms of algae, in relation to successional changes. Determining the autecological roles of periphytic species is preferable to listing species occurrences (for example, Hudon and Legendre 1987). SEM of periphyton communities is useful in the analysis of the 3-D structure and species interactions (see Hoagland et al. 1982). Jørgensen and Revsbech (1983) analyzed the microzonation within cyanobacterial mats using SEM and microelectrodes to measure photosynthetic rates. It is apparent that future studies involving SEM of intact periphyton will clarify our understanding of periphyton community structure and function.

Many investigators have estimated periphyton biomass of individual species from cell counts and biovolume estimates. Biovolume is a very important measurement, since cell numbers do not account for size differences. However, biovolume does not take into account the variable extent of inert cell walls and cell vacuoles. Sicko-Goad et al. (1977) stated that the actual metabolizing biovolume may vary between 30–82% of the total cell biovolume. Measures of cell surface area do not account for the fact that cell surface area is not linearly related to cell biomass. Clearly, measurements of biovolume, cell surface area, or AFDW yield different estimates of periphyton biomass.

To homogenize a periphyton sample for enumeration, samples may be shaken or treated ultrasonically to disperse aggregations (Gale 1975). Other researchers have used blenders for short periods (<45 s) to shorten algal filaments and disperse aggregates (Sumner and McIntire 1982). Biggs (1987) compared blending and shaking, and found that precision in cell counts was significantly improved by blending for 1 min. There was no significant difference between chlorophyll *a* concentrations or AFDW for the two treatments.

Much of the published literature on periphyton deals only with diatom communities. This is due, in part, to the fact that diatoms are ubiquitous, diverse, and have defined ecological characteristics, in as much as these are known (Stevenson and Lowe 1986). Consequently, diatoms have proven useful in water quality monitoring (Lowe 1974). Diatom frustules are taxonomically diagnostic and exhibit little phenotypic variation compared with other heteromorphic algae (Stevenson and Lowe

1986). Permanent, quantitative diatoms mounts are commonly made with Hyrax™ (Custom Research and Development, Auburn, CA) and allow easy comparison with herbarium collections. Separation of diatoms from large amounts of organic detritus, or epiphyte/macrophyte samples is easily achieved by oxidizing the samples. This method is not recommended for samples with large amounts of dead diatoms, as no distinction can be made between diatoms which were dead or alive when sampled. However, the ease with which diatom samples may be treated, identified, and enumerated should not encourage researchers to only consider diatoms in all types of investigations, as diatoms are not necessarily the most abundant or ecologically important group of algae.

Size of Sample

The area scraped or sampled was quite variable; most samplers removed algae from a relatively small area (<8 cm^2). The majority of epilithic sampling methods either involved scraping a template-delimited area of the rock surface with a brush or scalpel (Blinn et al. 1980), or scraping the entire upper surface of the rock. If the entire surface of the rock was sampled, the surface area was typically determined planimetrically (Elwood and Nelson 1972), or by fitting aluminum foil to the scrubbed area, and measuring the foil with a planimeter (Ennis and Albright 1982). Lay and Ward (1987) sampled periphyton from the entire rock and measured the surface area by pressing a 1-cm^2 inked stamp to the rock until it was completely covered, then counted the squares for a rough estimate of surface area.

No study has completely addressed the size of the sample necessary to accurately sample a heterogeneous periphyton community. Morin (1985) analyzed published data on densities of stream benthos, and many of his conclusions are applicable to studies of periphyton. He pointed out that preliminary experiments would establish the scale of the patchiness and variance at a site, and the size and number of samples could be adjusted accordingly. Wilmotte et al. (1988) estimated the minimal sample size for a marine epiphytic community, based on the stabilization of the species-area curves, and similarity coefficients. In that study, a sample of only 7–10 mm^2 met the needs of the experiment. However, they caution that minimal sampling areas vary with the community, as well as seasonally. Unfortunately, preliminary sampling is often not done, and Morin suggests that the researcher must often choose the number and size of samples based on several factors. Sampling is constrained by variables such as funding, and the requisite precision, dictated by the hypotheses in question and the magnitude of effect to be detected.

V. Methods for Measuring Primary Productivity

Measurements of periphyton primary productivity have received much study since the 1940's, when Lindeman (1942) introduced the concept of "trophic dynamics." Odum (1957) conducted one of the classic studies on Silver Springs, Florida, including, among other things, periphyton productivity, estimated from diurnal changes and oxygen concentration, and transfer of energy to higher trophic levels. A description of the early work on periphyton productivity up to the mid 1960's is given by Wetzel (1965).

Historically, measures of periphyton primary productivity were extrapolated from measures of standing crop. This method is not universally accepted because it does not take into account the turnover time of the community, and losses due to herbivory, or sloughing. To make direct measurements of primary productivity, researchers have traditionally measured either the production of oxygen (O_2 method) or the uptake of radioactive carbon (^{14}C method). In the following discussion, traditional methods will be classified by periphyton community, because the limitations of each method are closely related to the substrate morphology. Newer microelectrode techniques, measuring primary productivity of both benthic and epiphytic periphytic communities will follow the discussion of the traditional methods.

A variety of methods have been developed for use in aquatic systems depending on the rate of production and type of substrate. Most of the methodology was developed for use in stream systems, perhaps to disprove the axiom that stream production is primarily allochthonous. While lotic studies predominate, most of the methods discussed here can also be used in lentic habitats.

Primary Productivity of Epilithon

Many of the earlier studies on periphyton primary productivity such as those done by Brock and Brock (1967; ^{14}C method) and Odum 1957; O_2 method) involved removing the periphyton from the substrate, and incubating it in bottles either in the field or the laboratory. Only a few recent studies followed this method (Cuker 1983), because it is generally agreed that the primary productivity of the disturbed community is not identical to the undisturbed community due to changes in flow regime, nutrient supply, and disruption of the community architecture.

In situ studies have used chambers in which the substrate was placed in an enclosed chamber, chambers which were pushed into the benthic substrate, or domes which were sealed to bedrock or large rock surfaces. The simplest design is a Plexiglas box, into which the rocks are placed (Schindler et al. 1973). The chamber is incubated for an appropriate period of time, and productivity may be measured either by O_2 or ^{14}C method.

For studies that have either taken place in streams, or shallow and wave-impacted zones of lakes, the lack of circulation in a simple chamber may result in a decreased productivity. In a commonly cited paper, Rodgers et al. (1978) described an in situ chamber with an internal variable speed pump to insure complete mixing of ^{14}C and simulate stream flow. They experimentally compared periphyton primary productivity in static chambers and circulated chambers and showed that static chambers resulted in significantly lower primary productivity. This method has been used extensively in stream systems (Hornick et al. 1981; Hill and Webster 1982; Keithan and Lowe 1985; Mulholland et al. 1986). A simpler method for achieving internal circulation is the addition of a small "paddle" outside of the chamber, connected to another inside the chamber (Bombowna 1972). This mechanism should result in similar water velocities both inside and outside the chamber.

To measure productivity in areas with gravel substrate, small bottomless chambers have been pushed into the substrate (Busch and Fisher 1981); larger areas have been enclosed by 1×1 m skylights (Pennak and LaVelle 1979). In both of these studies, primary productivity was measured by withdrawing water for determination of evolved oxygen.

Loeb (1981) described an in situ method for measuring primary productivity on large rocks (>25 cm diameter) or bedrock (Fig. 1d). A Plexiglas hemisphere weighted with a lead

ring was sealed to the rock substrate with a neoprene seal, enclosing 200 mL of water, and covering 50 cm^2 of the substrate. This dome had an injection port for injection of ^{14}C, a bulb to allow mixing of ^{14}C, and two corked ports to allow flushing of contaminated water after the experiment. Turner et al. (1983) described a similar rectangular chamber. Unfortunately, no one has devised a similar chamber with internal circulation which works well on large rocks, and is relatively inexpensive, allowing suitable replication.

Primary Productivity of Epiphyton

Measuring primary productivity of epiphyton on living plants has methodological constraints which do not encumber experiments on epilithon. Because of this, many measurements have been made on epiphyton which has been scraped from the plant (Kowalczewski 1975; Jenkerson and Hickman 1983b; but see Brock 1970). Gons and van Keulen (1983) measured primary productivity after removing epiphytes by stirring and then lowering the pH to 5 to remove the tightly adhering epiphytes. The effect of disturbing epiphyton is not clear. In the only published study to date on the effect of removing the epiphytic community from the plant substrate before incubation, Hooper and Robinson (1976) found no significant differences in mean productivity between scraped and unscraped treatments, but very high variance may have obscured any treatment effects.

Kairesalo (1980) measured primary productivity of intact epiphyton on *Phragmites* in bottles using a ^{14}C method. After the incubation, epiphyton was removed from the stems by scraping. The oxygen evolution method could not be used in this type of experiment because of the combined production by the plant and epiphyton. Meuelemans and Heinis (1983) did use the O_2 method to measure epiphyton productivity because dead reed stems were the substratum.

In two of the few studies of this kind, Cattaneo and Kalff (1979) and Haines et al. (1987) described in situ measurements of epiphyton primary productivity on *Potamogeton richardsonii* and reed stems using hinged, cylindrical chambers (Fig. 1e). These chambers were divided into two halves and closed around the plant underwater. The Haines chamber sealed around the intact reed stem with neoprene, through which the ^{14}C was injected. These chambers have obvious value in in situ studies of epiphytic productivity, but necessitate some floatation when used on macrophytes with lightweight, flexible stems.

Primary Productivity of Periphyton on Artificial Substrates

Intact, small artificial substrates (glass or plastic slides, acrylic rods) have been put in glass bottles for measurement of primary productivity using either the O_2 or ^{14}C methods (Allen 1971; Rodgers and Harvey 1976; Goldsborough et al. 1986). Hooper-Reid and Robinson (1976, 1978a) measured primary productivity of periphyton on cellulose acetate strips in bottles. The use of the strips facilitated later analysis, as the strips dissolved in dioxane-based scintillation fluor with insignificant quenching. Generally, such productivity experiments are incubated in situ, and results from experiments which are not conducted in situ must be viewed with caution. For example, Peterson et al. (1983) incubated glass slides from an experiment in a stream in a nearby lake, in translucent tubes, with unamended stream water. Although the primary purpose of this experiment was to determine the differences between nutrient treatments in a flow-through stream bioassay, their results would not reflect in situ productivity.

Although ceramic tiles are being used extensively as artificial substrates, particularly in herbivory studies, few studies have incorporated measurement of primary productivity. In a novel approach, Stewart (1987) incubated tiles in 1-L plastic bags (Ziploc®). These bags are disposable after use, inexpensive, are easy to work with, and little O_2 diffuses out during a short incubation period.

Nutrient-diffusing substrates (flowerpots) have also been used in productivity measurements although the ^{14}C method presents problems when applied to this porous substrate. The rate of ^{14}C penetration into the pot is not known and the resultant concentration of ^{14}C in the water surrounding the pot is also unknown. Also, this technique would generate large amounts of low activity, solid radioactive waste. On the other hand, the O_2 evolution method is less problematic. Fairchild and Everett (1988) constructed small Plexiglas chambers which enclosed the substrates and the subsequent oxygen evolution was measured with a micro-Winkler method.

Limitations of the ^{14}C and O_2 Methods for Measuring Productivity

Both the O_2 and ^{14}C methods of estimating primary productivity have serious drawbacks. The O_2 method has been used extensively in the past because it is quick, easy, and inexpensive, and can be done in the field. Most commonly, the Winkler Method has been used (APHA 1985), although methods utilizing oxygen probes have recently simplified and increased the accuracy of the measurement. However, energy transfer in food webs is not expressed in units of oxygen, and therefore a conversion must be made to units of carbon. This includes many assumptions about photosynthetic quotient and respiratory quotient, which have not been experimentally resolved (Peterson 1980). In very productive systems, oxygen bubbles may form, causing an underestimation of productivity, while nonphotosynthetic organisms may affect the overall gas balance, and introduce further error.

The ^{14}C method is much more sensitive than the O_2 method, and the error in determining ^{14}C concentration is approximately 1% that for O_2 (Stevenson and Lowe 1986). Unfortunately, the use of ^{14}C is expensive, requires some training (general reference; Wang et al. 1975), and measurements generally are not done in the field. The ^{14}C method yields results which are generally considered to be somewhere between gross and net primary productivity because of refixation of intracellular respiratory CO_2 (Robinson 1983). However, for short incubations, ^{14}C uptake is approximately equal to net primary productivity (Peterson 1980; Hill and Webster 1982). Although it is advisable to measure dark uptake of ^{14}C, most researchers have found that dark counts are so low (<5% of the light counts), that dark uptake is not routinely measured (Jones and Adams 1982; Peterson et al. 1983; Mulholland et al. 1986). Additionally, in some instances, photorespiration may be quite high. Graham and Turner (1987) used DCMU, which inhibits photosystem II, in conjunction with ^{14}C incubations. In this experiment, productivity would have been overestimated by 30% if photorespiration was assumed to be equal to dark respiration.

A few published comparisons of the ^{14}C and O_2 methods have achieved higher productivity measurements using the O_2 method, and lower using the ^{14}C method (e.g. Schindler et al. 1973, lentic study). Some similar research yielded questionable results because the experimental conditions for each trial were

not identical (e.g. Hunding and Hargrave 1983; Bott and Ritter 1981).

Microelectrode Techniques for Measuring Primary Productivity

A critical assumption of both the ^{14}C and O_2 methods is that both the ^{14}C added or the O_2 produced by the periphyton mat are in diffusional equilibrium between the periphyton layer and the surrounding water. This has shown to be false except when the periphyton mat is very thin (Sand-Jensen 1983). Before the development of oxygen microelectrodes, the traditional methods to some degree underestimated productivity of periphyton because an equilibrium does not necessarily exist between the interstitial water and the surrounding water. Carleton and Wetzel (1987) discuss four processes causing this disequilibrium: (1) oxygen production by periphyton; (2) diffusion of oxygen affected by turbulence and oxygen gradients; (3) respiration by microorganisms in the periphyton mat; and (4) possible interactions between periphyton and the substrate. The use of oxygen microprobes, with resolutions of 100 μm and 1 s allow experimental determination of each of these microprocesses. An excellent discussion of the application of microelectrodes in microbial ecology, including productivity is given by Revsbech and Jørgensen (1986). Other useful references include Grainger and Forstner (1983; Jørgensen and Revsbech (1983); Revsbech et al. (1983); Carleton and Wetzel (1987); and Revsbech (1989).

Revsbech and Jørgensen (1986) detail the types, design and construction of oxygen, sulfide, and pH microelectrodes. Two types of oxygen electrodes are commonly used: the cathode and the Clark type, and both can be made with tip diameters of <1 μm. Problems with the cathode type electrode have led these and most researchers to use the Clark type which has a comparably fast response time (<0.2 s), but a relatively more stable signal.

To date, microelectrodes have typically been used in the laboratory under conditions simulating ambient conditions. An experimental setup for measuring productivity in benthic communities has been described by Revsbech and Jørgensen (1986). Samples were held in a water bath, and micromanipulators moved the microelectrode, allowing a depth resolution of <10 μm. Typically, the microelectrode was first positioned above the periphyton mat and advanced downward. The electrical current in the circuit at various depths was recorded on a strip-chart recorder. A schematic was given for computerized data collection and display from the microelectrode circuit and other apparatus such as light intensity and other analog signals.

All of this equipment is usable in the field, on solid surfaces, and under fair conditions with low air humidity. The authors suggest that the standard apparatus can be modified for field conditions. For example, an amplifier built into the electrode holder alleviates excessive electrical noise due to ship vibrations or wind. Measurements have also been done in water at depths requiring a diver to operate the micromanipulator. Revsbech and Jørgensen do comment that work in regions with many macroscopic organisms may be difficult, as snails, crabs, and fish often approach and break the microelectrodes. Smaller benthic animals within the mat may disturb the microgradients.

Microelectrodes are very useful in measurements of epiphyte primary productivity. Rather than separate the epiphytes from the macrophytes, which undoubtedly alters the physicochemical environment and metabolic rates as well, Sand-Jensen and Revsbech (1987) used microelectrodes to measure epiphyte productivity at varying light intensities in the laboratory. So far, measurements have been done on excised leaves pinned to an agar plate to provide a firm surface, as any field techniques would necessitate an apparatus to hold the leaf. The preceding study, as well as a similar study (Sand-Jensen et al. 1985) indicate the importance of measuring epiphyte productivity with microelectrodes. The microzonation of the algal production can be clearly delineated, and the algal and macrophyte productivity can be distinguished (up to 0.1–0.2 mm from the macrophyte surface) without disturbing the integrity of the association.

Other Methods for Measuring Primary Productivity

Early researchers used measurements of periphyton biomass accrual to estimate productivity. Bothwell (1985) points out that "biomass accrual estimates of primary production have been the hallmark of periphyton research," but that this is a very questionable practice. Murphy (1984) demonstrated that bioaccrual on artificial substrates was only about 2% of the measured net primary productivity on cobbles in a coastal stream. This is often attributed to the complication of unknown turnover time of the periphyton and unmeasured losses due to herbivory, sloughing, or mechanical dislodgement. However, this method may be used to roughly estimate productivity in systems with rapid growth or low loss rates.

Open stream methods have been used, particularly in streams with a variety of substrate types and heterogeneous algal distribution. Stockner (1968) and Lewis and Gerking (1979) based productivity measures on changes in daily dissolved oxygen curves. Cushing and Wolf (1984) chose the diel pH–CO_2 curve method because little turbulence occurred in their stream and they considered the CO_2 exchange with the atmosphere to be negligible. However, these estimates necessarily include invertebrate respiration, in addition to periphyton primary productivity and respiration, which may lead to large errors. In addition, the lack of reliable estimates of gas exchange rates may lead to erroneous productivity in open stream methods. To alleviate the problems of unknown exchange rates, Gregory (1980) used a total inorganic carbon measurement to estimate production by epilithic stream periphyton in chambers.

Elwood and Nelson (1972) added ^{32}P to a natural stream, in concentrations high enough to monitor periphyton production and loss rates for 6 wk utilizing a material balance method. This method was very effective for measurement of net productivity, standing crop of periphyton, and grazing rates. Because of the relatively short half life of ^{32}P (14.3 d), there was little danger of continued contamination. However, Gregory (1974) found this method to be less successful in a high gradient stream due to high cost and intensive sampling regime.

VI. Recommendations

From the preceding review of field methods employed in periphyton investigations, several recommendations can be made regarding the choice of methods in future research. First, artificial substrates should not be assumed to mimic the naturally occurring substrates unless this is shown to be true experimentally, and artificial substrates should not be used in research where they are expected to mimic the natural substrates; i.e. periphyton biomass and productivity estimates, or surveys to determine species composition. On the other hand, artificial

substrates are extremely valuable in research on community development, in comparisons of environmental variables and comparisons between environments, and in experiments where no naturally occurring firm substrate occurs or can not be a part of the experimental design. The decision to use naturally occurring substrates or artificial substrates in studies of herbivory is critical. Artificial substrates such as tiles usually decrease substrate heterogeneity, and allow more complex experimental designs, but when artificial substrates are used, the effect of the substrate on herbivores must be considered.

A second recommendation concerns the use of terminology in published reports on periphyton research. In the past, the adjectives epilithic and epiphytic were used when the periphyton was actually sampled on artificial substrates. The terms biomass accrual, production, and productivity are often confused, or used interchangeably. Standing crop or biomass is the weight of the plant that can be sampled or harvested by normal methods. Primary production is the net change in plant biomass, including any losses, over a given period of time. Productivity is production over time, or the rate of production.

Also, distinctions between net and gross primary productivity are critical when comparing productivity measurements made with the O_2 and ^{14}C methods. Traditional methods of measuring periphyton productivity yield a mean community value. By combining microelectrodes with light and electron microscopy, resolution is greatly increased, and future studies may measure in situ productivity of individual species within a heterogeneous community.

Future advances in microelectrode technology hold exciting applications in periphyton research. Novel types of sensors such as those which simultaneously measure light, temperature, and oxygen are certain to be developed and applied to productivity or other physiological studies. Improvements in microprocessor technology, remote controls, and amplifiers will allow faster and more accurate data collection, especially under field conditions.

In conclusion, there is not now, nor will there probably ever be a narrow set of standard methods which are accepted by all researchers or appropriate for all investigations. Experimental methods will continue to be constrained by time available, laboratory equipment, as well as funding. Therefore, it is important for researchers to accurately describe their methods and justify their use, so that other researchers can use this information to make informed decisions on methods for future work.

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